AMAZONIANA	II	4	449—495	Kiel, Dezember 1970

(From: Cooperation between Max-Planck-Institut für Limnologie, Abt. Tropenökologie, Plön, Germany, and Instituto Nacional de Pesquisas da Amazônia, Manaus-Amazonas, Brazil)

Investigations on the Ecology and Production-Biology of the „Floating Meadows" (Paspalo-Echinochloetum) on the Middle Amazon[1])

Part I: The floating vegetation and its ecology

by WOLFGANG JUNK, Max-Planck-Institute for Limnology, Department Tropical Ecology, Plön, Germany

Contents

[1]) Brazilian Contribution of the International Biological Programme, Section PFM; Contribuição brasileira ao Programa Biológico Internacional, Secção PFM.

Introduction

A traveller on the Amazon often meets large quantities of floating plants which either individually or more or less in big islands are drifting down the river. Sometimes there are so large quantities of them, mixed with branches and trunks, that the motor-boats have carefully to navigate through them. To his great surprise the onlooker also notices that often large, densely covered areas at the bank wave up and down according to the undulation of the river surface and therefore the real bank-line does not agree always with the outer margin of the vegetation. Further it is really striking that the major part of this floating vegetation consists of grasses, and thus the term "Floating meadows" was coined for it (Gessner 1959, Marlier 1965, Sioli 1968). This phenomenon is unusual for a foreigner because of its novelty and large dimensions; for the local population, the floating meadows are really of practical importance. On the one hand the floating grasses are used as cattle fodder, especially during the high water level when the main part of the pasture-ground is flooded and the remaining areas are destroyed by the tread of the wandering cattle, and they are often the only food for cattle and horses. Thus grasses drifting down the river are hauled ashore by boats, and grass areas in the shoreland lagoons are also regularly cut with machetes from the boats and collected (O'Reilly Sternberg 1966, Wilhelmy 1966). On the other hand the region of floating plants offers lots of fish which play an important role for the nourishment of the human population. Especially the Pirarucú (*Arapaima gigas*), an economically important and valuable commercial fish, likes to stay near or beneath the floating grasses where the inhabitants spear them. Many a times the "floating meadows" are a handicap to the boat-traffic by obstructing narrow canals or mouths of lakes or by getting entangled in the propellers and rudders. At times boats are also saved from storms under their cover, as the waves are reduced through the entangled stems.

Thus the floating vegetation represents a phenomenon of the Amazon which influences the appearance of the landscape in a very characteristic way and plays an important role in life of the population.

In books of travels of the last century the floating vegetation is mentioned again and again (Agassiz 1869, Wallace 1889, Spruce 1908 and others); detailed information or special descriptions, however, are only given in rare cases (Doell 1877, Miranda 1907, Spruce 1908, Le Cointe 1947). A summary of knowledge about the aquatic and semiaquatic species of the Gramineae-family is presented by Black (1950). He makes statements about existence, utilization and state of the single species in the system. More recent data can be found in Gessner (1959), Marlier (1965) and Sioli (1968). For the first time Marlier gave quantitative information on the primary production in the zone of floating plants in Várzea lakes and on the biomass of the aquatic fauna in its root system.

This paper (Part I) presents the results of observations made on the ecology of the floating vegetation, while in the second part the quantitative and qualitative aspects of the aquatic fauna of this special biotope will be examined. Further, the environmental factors which have a decisive influence on it will be discussed there.

The research was supported by the Max-Planck-Institute for Limnology, Department Tropical Ecology, Plön, and the Instituto Nacional de Pesquisas da Amazônia (I. N. P. A.), Manaus, as a cooperative contribution to the Brazilian IBP.

Acknowledgements are due to the above mentioned authorities for their assistance and information contributing to my research work. My grateful thanks are due to Prof. Dr. Harald Sioli, Director of the Max-Planck-Institute for Limnology, Department Tropical Ecology, Plön, who made it possible for me to stay in Manaus and at the Amazon for 20 months, from April 1967 to October 1968, and I am indebted to Dr. Djalma Batista and Dr. Octávio Mourão, successively directors of I.N.P.A., Manaus, at that time, for providing facilities for my stay in Amazonia and for their interest and encouragement in the research work. And last but not least, my thanks are due to Dr. Byron de Albuquerque of I. N. P. A. who made the determination of the plants, to Senhor Antônio José dos Santos and Senhor Umbelino Jorge de Oliveira for their valuable assistance in my field-work in Amazonia.

I. General characterization of investigation area

a) Geological-geographical survey

The geology of the Amazon basin and its marginal territories was treated more specifically by Katzer (1903), Oliveira and Leonardos (1943), Sioli (1956), and others. Therefore here only a rough outline will be given.

During the Paleozoic, there was a wide bay of the Pacific Ocean, open to the west and sealed in the east, which extended between the Archean shields of Guiana and of Central Brazil. The sediments deposited during Presiluric to Carbonic periods appear at the earth surface today in the marginal territories of Lower Amazonia along the fringes of the granite- and gneiss-massifs of Guiana respectively of Central Brazil. Towards the end of the Neocarbonic period, the sea retreated. During the Mesozoic the whole territory remained dry and was drained into the Pacific by rivers. In this period penetrations of diabase took place, which most frequently reached the surface of the earth in the carboniferous strips of Lower Amazonia. In the Miocene period the Andes rose, gradually closing the basin to the west and thus forming a huge inland lake, which deposited sandy-clayey fresh-water sediments of a thickness up to 300 m. Towards the end of Pliocene or only in Pleistocene the water masses forced their way towards the east and the lake drained off into the Atlantic. The Amazonian rain forest of today developed on the drained lake bottom. The rivers digged their beds into the deposited soft fresh-water sediments. As an explanation for the striking width of the lower courses of most affluents of the Lower Amazon, Sioli (1956) assumes that the river disposed of a steeper gradient due to the subsidence of the sea level during the glacial periods by about 75 to 100 m and thus could work out their deep and wide beds. As the Amazon basin has only a slight gradient, the raising of the sea to its actual level at the end of the last glacial period dammed the water masses of the river up till far back in the country. So at Manaus — about 1500 km distant from the Atlantic coast — the water level of Rio Negro, according to the season, is only about 14 to 30 m higher than the sea level. This means that the lower courses of the lower Amazonian rivers must be regarded as drowned valleys which, according to the quantity of sediment transport, have already been or are still being refilled with recent alluvia by the rivers.

Nature and quantity of sediments as well as transport of dissolved substances are dependent on the drainage area of the waters. Thus the rivers with an Andean drainage area are strongly loamy-muddy by large quantities of inorganic suspended matter which is carried along. The transparency of the Amazon, measured with the Secchi-disc, for example lies only between 25 and 40 cm, the transport of suspended solids being 50 to 150 mg/l (Sioli 1967). In contrast to this the waters coming from the strongly levelled

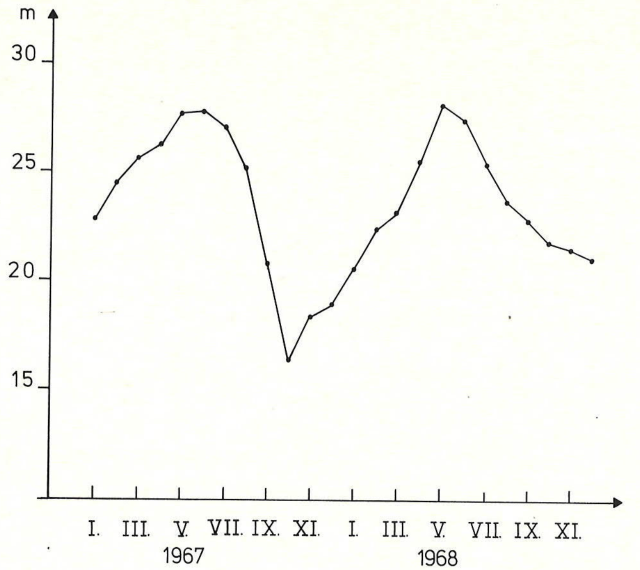

Fig. 1: Annual water level fluctuation in Rio Negro at Manaus

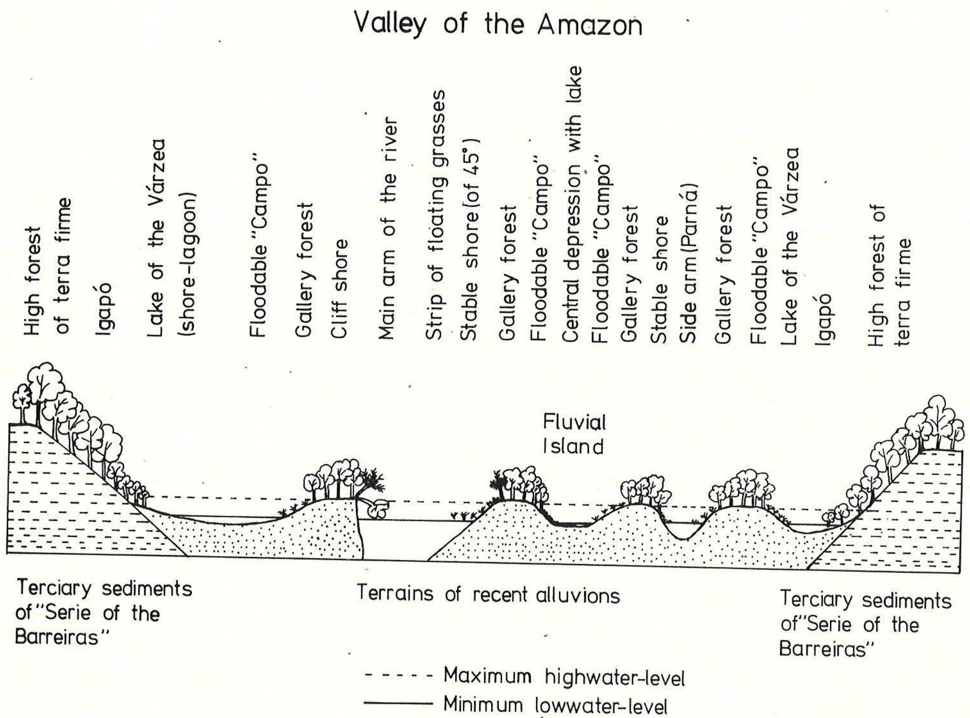

Fig. 2: Schematic cross-section through the Lower Amazon valley; height exaggerated (From Sioli 1964 b).

massifs of Central Brazil and the Guianas or from the region of tertiary fresh-water sediments — which form the "Terra firme" of the Amazonian flat land — are transparent and either colourless or deep brown by dissolved humus substances. From this Sioli (1950) deduced the following three water types of Amazonia.

1. rivers with large quantities of inorganic sediments and loamy-muddy colour = white-water-rivers (i. g. the Amazon);
2. rivers with small quantities of inorganic sediments and transparent, greenish colour = clear-water-rivers (i. g. Rio Tapajós);
3. rivers with equally small quantities of inorganic sediments but with large quantities of dissolved humus substances, and brown to red-brown in colour = black-water-rivers (i. g. Rio Negro).

Especially the white-water-rivers with their great sediment load, filled their broad valleys up with alluvia in recent times, thus depositing in them a wide alluvial land which is still subject to continuous overforming and shifting. This alluvial land is called "Várzea". It extends as far as the influence of high water can reach, and at the Solimões-Amazon[1]) it covers an area of 64,400 km², with a breadth of 20 to 100 km (Lúcio de Castro Soares 1956). Due to seasonal differences in the quantities of rain and to the melting of snow in the Andes in springtime, the Amazon is subject to strong annual fluctuations of its water level. Although because of the enormous extension of the drainage area (more than 7.000 000 km²) the large affluents often reach their peak level at different times and thus the amplitude in the main river itself is reduced, the annual level fluctuations at Manaus nevertheless come up to 16 m (Fig. 1).

The great fluctuations of their levels intensify the landscape-forming power of the rivers, which is due to enormous discharges and to strong currents. At low water level, approximately from September to January, big and often kilometers-long pieces of the bluffs covered with vegetation come tumbling down into the river (so-called "terras caidas"). These land masses are washed away by water and get re-deposited in the places near the banks protected from the current and often spread over many square-kilometers. The main mass of the sediments is deposited on the embankments near the river forming levees which are covered with trees; behind, the soil slightly slopes away and gives rise to many lagoons, which can reach a length of more than 100 km and a width up to 40 km and extend land inward to the terra firme-side. In this way the typical várzea-landscape develops with a nearly incalculable, continuously changing complex of lakes, islands and canals (Fig. 2).

There are close relations between the chemistry of the waters and that of their drainage areas. Thus the chemistry of the Amazon is influenced by the Andes, by the intensive activity of erosion in the mountains and also by relatively large amounts of electrolytes being washed out of the weathering crust together with large quantities of fresh sediments. This means that the annual high waters also lead to a continuous new supply of electrolytes in the inundated area which makes the várzea look completely different from the surrounding terra firme in regard to the composition of the flora (Huber 1909, Ducke and Black 1953, Hueck 1966 a. o.). The Amazon water has a

[1]) From the mouth of the Atlantic to the mouth of Rio Negro the Amazon is called Amazon, from there to the Peruvian border it is called Solimões and then, in Peru, Marañon.

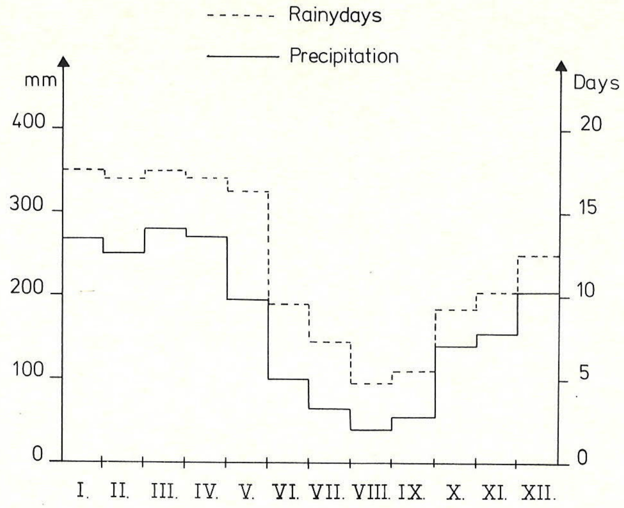

Fig. 3: Monthly precipitation and the number of rainydays per month at Manáus (from Reinke 1962)

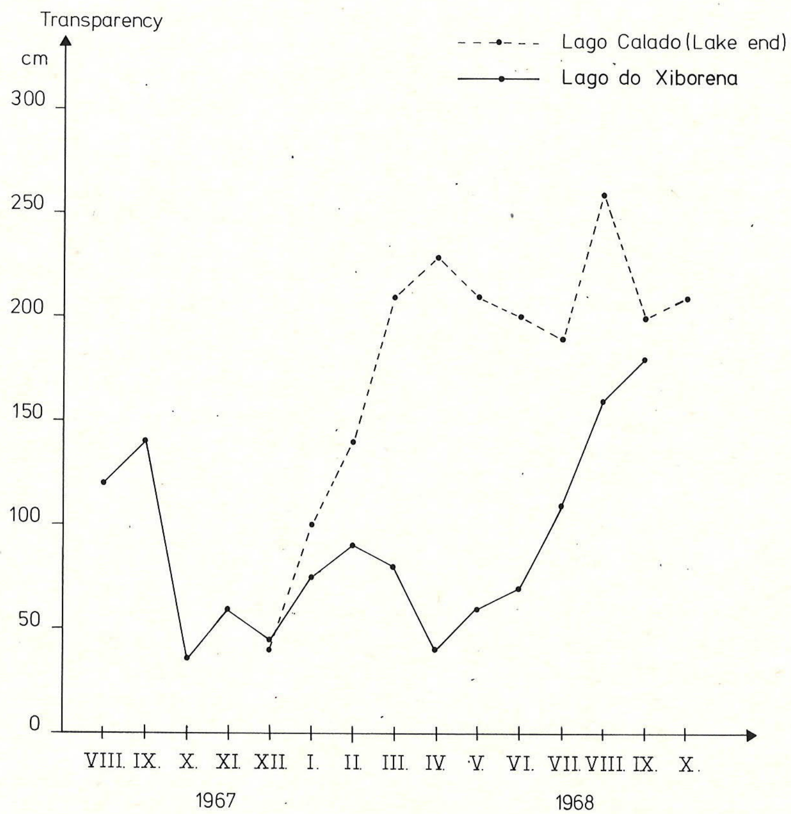

Fig. 4: Fluctuation in transparency in 2 Várzea lakes

content of electrolytes of about 60 μS_{20} and a pH of about 6,8, whereas the waters of the surrounding tertiary terra firme are acidic and remarkably poor in electrolytes (elecctrical conductivity of 8—12 μS_{20}; pH around 4,5).

b) Climate

The climate of the middle Amazon is characterized by a distinct, relatively dry „summer" and a rainy "winter" (Fig. 3), as the respective seasons are called. The dry period lasts from July to September, and the wet season form December to May. The months of June, October, and November form a transition period between these seasons. The higher rainfall, as well as the number of rainy days are remarkably higher in the wet season than in the dry season. Both curves in the graph run approximately parallel to each other (Fig. 3). The average rainfall amounts to 2127 mm (mean of 25 years).

The large extent of water areas, the closed cover of virgin forest and the frequent rainfalls imply a high content of atmospheric humidity. In April the relative atmospheric moisture is around 82,3%, and in September it is around 73,7% (Reinke 1962). The decrease in precipitation during the dry period is expressed also in the amount of atmospheric humidity.

This everlasting humid air on the Amazon-lowland prevents on the one hand an extreme rise of temperature during the day, as it happens in dry tropical climates, but on the other hand there is a strong irradiation at night, so that the temperature only slightly decreases. The daily variation is in the order of 8—10° C, Schröder (1955). Considering the high atmospheric humidity the fall of temperature is sufficient for an important dew-fall in the early morning hours during the dry period. In Manaus the mean annual temperature is about 27,2° C. The maximum value indicated by Reinke (1962) is 37,8° C. During the short-term invasion of cold air masses from the winter in the southern hemisphere (Patagonia), occuring annually once or twice between May and September, the temperature may drop below 20° C, causing fish mortality in the lakes (Geisler 1969). On the contrary the difference between the mean temperatures of the dry and rainy seasons is only 1,6° C (September and March). Thus the daily amplitudes are higher than the annual amplitudes. Therefore middle Amazon belongs to the region with a diurnal climate. According to the Köppen classification (1931) the region ranges within the Ami-type. This type comprises those zones in which in spite of a dry season a tropical rainforest exists.

II. Importance of water-level-fluctuations for the Vegetation

a) Terrestrial vegetation

Besides of the chemistry of the waters the great water-level-fluctuations turn out to be especially important for the flora of wide várzea-areas. At low water-level, approximately from September to January, large areas remain dry, then becoming covered again by 10. and more meters of water during some months of highwater season. During the dry period the vegetation of these areas can develop on the one hand from seeds, brought there by wind, birds etc. from drier places, but on the other hand also from plants which either themselves or by seeds can survive the time of inundation. These are capable of getting through their whole cycle of development within the more or less short dry period or, as for perennial plants, of getting to seed ripeness in the same season. Many times the seedlings must be in a position to bear the intensive solar radiation on the extensive shadowless areas. The plants themselves, i. e. several species of the Gra-

mineae-family, either die away in the rising water and then partially cover the surface of the lakes with their rotten stems at rising water level, or they survive under water until the next dry period sets in. In this case they can already be classed with the semiaquatic vegetation (*Paspalum fasciculatum*). In the same way the Igapó (Inundation Forest) of the várzea — being completely different in species composition from the Igapó of the black waters — represents an adaptation of this kind. As to the settlement sequence of the stock of trees on newly developing banks of alluvial land, more exact information is given by HUBER (1909). Further data can be found in HUECK (1966).

b) Aquatic and semiaquatic vegetation

For the settlement of aquatic and semiaquatic vegetation the high water level fluctuations are also of decisive importance. Exclusively submerged forms being rooted in the ground can easily get dry at falling water, at rising water, however, the light conditions quickly deteriorate, as the depth of visibility (measured with the Secchi-disc) is not very great in the lakes (Fig. 4). Subject to the morphology of the lake it may happen that under the influx of fresh Amazon water from time to time the degree of visibility is further appreciably decreased owing to richness in sediments (Fig. 5). Thus it is not striking that higher, exclusively submerged plants play a rather small role in the várzea-region. In the lakes of the surroundings of Manaus only *Utricularia sp.* (Family Lentibulariaceae) was found.

Under these environmental conditions, however, the development of the floating vegetation reaches gigantic extents. Floating forms can be regarded as being optimally adapted to the conditions in the várzea in so far as they always remain — in spite of the continually changing water level — in the light climate, which is optimal for them. Although also in this case an absolute dry-fall often effects the decay of the plants, the development of masses, however, makes the survival of parts of the population possible in the remaining water-accumulations and at humid places; with rising water these parts vegetatively increase explosion-like, gaining their former population density within a short time. Furthermore, seeds and spurs respectively also get to germination, but it must be pointed out that in an aquatic and semiaquatic vegetation the vegetative reproduction plays a far more important part than the sexual reproduction with regard to the increase of the population.

Whereas the falling dry of the lake bottom signifies the death of merely aquatic floating forms, it just offers to a group of semiaquatic plants the possibility to populate this biotope. As mentioned before in the preceding chapter, it is difficult, however, to draw the line between land- and water-vegetation in the Amazon region, and in several plant families there are sliding transitions (e. g. Gramineae, Cyperaceae, Leguminosae).

III. On the Ecology of the population-forming species

The ecological observations over a period of 18 months, (2 periods of high water and 1 of low water), made on the aquatic and semiaquatic vegetation shall be presented here in this chapter. Only those species are taken into account which are of importance in the surroundings of Manaus.

a) *Paspalum repens* BERG (Fam. Gramineae)

Brazilian name: Pirimembeca (Piri = grass, membeca = soft), after LE COINTE (1947) and BLACK (1950) also Canarana rasteira. *Paspalum repens* is the species of grass that

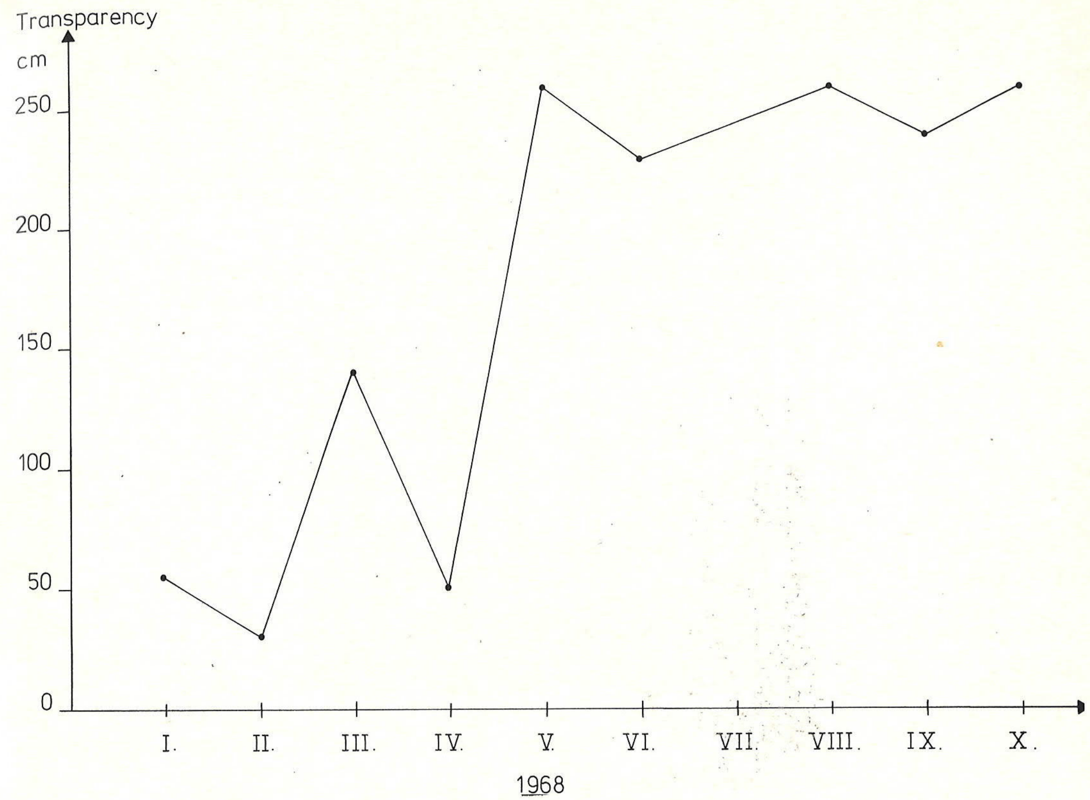

Fig. 5: Lago Calado (mouth): Inflow by shoves of white water (January to May)

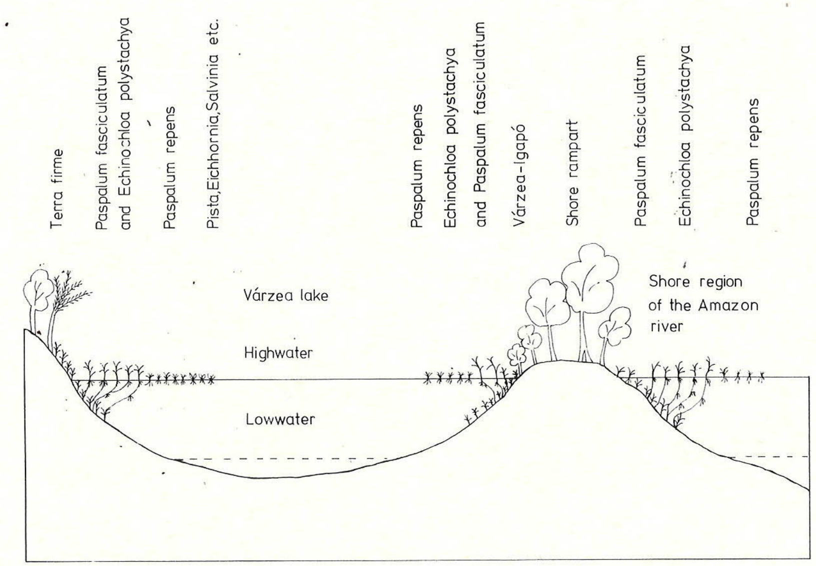

Fig. 6: Vegetation of a typical Várzea lake with high oscillations of water level (Schematic)

Photo 1: Growth of floating root clusters of *paspalum repens* in a Várzea-Lake.

Photo 2: Different types of growth of *paspalum repens* from left to the right: 1) Young stage with blister-like swelling on the leaf base, 2) Older stage with reduced blister-like swellings on the leaf base, 3) Hard, thin sprout from an old population, 4) Land form.

besides *Echinochloa polystachya* mainly contributes to the development of floating islands which are drifting down the Amazon. The grass can be found in large quantities as well in the Amazon itself as in the várzea-lakes. It also appears in Rio Tapajós and in Rio Madeira. Furthermore, Black (1950) mentioned British Guiana and Columbia as habitats, Gessner (1959) reported populations in the Orinoco-delta. This species is regarded as good fodder for cattle and horses.

Development within the course of the year:

With rising water about December an explosion-like development of populations begins. The young plants developing from seeds form an unramified stem of up to 1 m length and 2 mm thickness with 20 to 40 cm long internodes which at their ends carry a cluster of shoots with leaf-sheds as floating organs that are swelled up blister-like. Within this range the internodes are only 1 to 3 cm long, the stems are about 5 mm thick. The stem ramifies in each node, forming there a new shoot. The thin, unramified stem touches the ground, and breaks after some weeks by the influence of wind and currents. From last year's remnants which have survived other plants grow on the drained ground or in water pools.

It is a striking fact that at that time there appear two obviously different forms. One of these is equally green and hairless, whereas the other one, with violet spots, possesses fine bristles, mainly at the leaf-sheds. After few weeks both forms start blooming, the spotted form blooming more extensively during this period, and develop short-stemmed blossoms and seeds being capable of germination. In a laboratory test about 25% of the seeds germinated after three weeks, the development, however, couldn't be followed. The spotted form completely disappeared after approximately 2 months and was not observed again during the high water period.

After the first 4 to 6 weeks, when the grass is only forming short internodes, the growth changes and the internodes increase to a length of about 10 cm and a thickness of 7 to 10 mm. Floating bunches of roots, which may get to a length up to 80 cm in the lakes and firmly connect the particular stems among one another, are formed at the nodes (Photo 1). During the next 4 to 5 months the increased growth continues, forming a dense mat which is completely detached from the ground. During this period flowering plants are seldom found. The stems can grow very long, and it seems nearly impossible to detach plants completely from the entanglement. Spruce (1906) reports a length of 45 feet (= 13,72 m) for one stem. According to our observations they may grow considerably longer than reported. Regarding the enormous rapidity of growth during the first 5 months it should be assumed that larger waters areas would be covered with grass in a relatively short time. This is prevented on the one hand by parasites which in masses attack the populations from time to time. Here we must especially mention *Diatrea saccharalis* (Lepidoptera, fam. Pyralidae) and *Chlorops sp.* (Diptera, fam. Chloropidae) whose larvae undermine the vegetation tips, thus reducing the rapidity of growth with particularly great success. Sometimes more than 50% of the shoots of the various populations examined were infested, and the plants remarkably began to die away. Thereby a little population at the Tapajós had nearly completely disappeared. But generally such mass attacks only last for a few weeks, so that the plants can recover.

Towards the middle of June the real flowering period begins. The vegetative tips and blossoms rise above the water level by 40 to 100 cm. The structure of the grass has kept on changing. It has hardened and the blister-like swellings of the leafbase have almost gone (Photo 2). The grass is now floating by means of the long hollow internodes. At the

Photo 3: Old stem of *paspalum repens* with clusters of hard, thin sprouts.

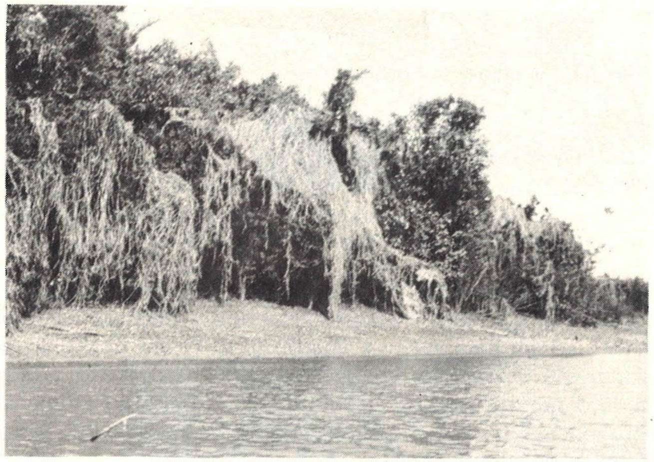

Photo 4: With falling water level — the *paspalum repens* population fallen dry on the top of the trees.

Photo 5: Old stem of *Paspalum repens* — with a land form on the nodes.

beginning of the main flowering period the growth considerably decreases and continues to a small degree only at the margins of the populations, so that from then onwards there is hardly a possibility for larger water areas to become overgrown. Very large quantities of seeds are produced, which after falling down, mostly get stuck in the root system, but there the seeds normally do not germinate. During the investigations on the animal population in the roots examined large quantities of seeds were found again and again, and only in very few cases germinating seeds were recorded. The factors limiting the germination of the seeds could not be studied at this stage. It might be possible that the seeds need a longer time of rest or of dry period before germination.

Soon after blooming has ceased, the grass populations partially "grow old". The parts standing above the water surface, dry up and collapse. Thereby, the shadows casted by the plants get reduced very much; this allows an infiltration of sun rays to a large extent onto the surface, and thus the temperature rises to more than 40° C, because through the dense root system the circulation of water is only possible at a reduced rate. The grass begins to get rotten and the high temperatures obviously support this phenomenon. Generally there is no decay in the less dense marginal region of the population, as at these places the population is young and there is a good circulation of water (compare p. 483ff). Inside the grass-area, at the nodes of the plants near the water-surface bunches of thin, hard sprouts develop, which grow up vertically and form a hard root system (Photo 3). With dropping water level the grass-areas partially drift out of the lakes into the Amazon, to a large extent they get stuck on the tops of the bushes in the várzea-igapó, which are flooded during high water level (Photo 4). The quantity of the grass dried up in this way is so large that, at a far way distance it almost gives the impression of an agriculturally utilized area (Gessner 1959).

A part of the grass falls on to the dry ground and here some of the sprouts and clusters of sprouts take roots and develop into a terrestrial form (Photo 5). This form is small, has hard stems about 2 mm thick and small hairy leaves. The blister-like thickenings at the leaf-base have completely disappeared. Some four or six weeks later, only a few 20 to 30 cm high clusters of the large populations can still be found among a lot of other grasses, these clusters being composed of several sprouts whose vegetative development could be regularly proved by the decaying rests of old stems (Photo 6). Consequently the terrestrial form of *Paspalum repens* is completely different from the aquatic form in its structure (Photo 2, p. 458). Another difference is shown in the water-content of the stems (Tab. 1), which in the aquatic form is noticeably higher than in the terrestrial one[1]). Young populations which are characterized by many shoots with an augmented leaf base and blister-like swellings possess the highest water-content. Old floating populations have evidently minor water-content; they are characterized by disappearing blistered leaf bases, comparatively off shoots, and slower growth. The difference in

Table 1: Water content of *Paspalum repens* stems

	Waterform young	Waterform old	Landform	
Date	6. 2. 68	6. 9. 68	6. 2. 68	2. 3. 68
Total stem-length	197 cm	573 cm	305 cm	474 cm
Stem-thickness	0,7—1 cm		0,2—0,5 cm	
Fresh weight	54,3 g	175,0 g	29,0 g	33,0 g
Dry weight	2,5 g	25,99 g	6,6 g	9,6 g
Water content[2]	95,4%	85,2%	77,2%	70,9%

1) Only stems were used, because the adherent inorganic suspensoids can easily be removed.
2) Of course, large quantities of stems are required for exact determination of water content.

water-content in the stems of the terrestrial forms can possibly be brought back to their origin in the different humidity-ratio of their localities.

Further morphological differences exist between plants growing in the running white-water of the Amazon rich of suspended solids, and those largely growing in cofined water. In running white-water the floating bunches of root clusters remain considerably smaller than in the lakes. The average dry weight of the roots of the root clusters in lake water is about 0,17 g and it is only about 0,05 g in running white-water (Tab. 2). Further, the roots in the lakes are twice as long as in the Amazon. Of course here as well the transitions between the both biotopes are fluctuating.

The differences indicated in the appearance of the forms can be traced back to the biotope as follows: in the Amazon itself the populations are exposed to the current and therefore they are continually supplied with new nutrients. On the other hand the roots act like filters and catch the suspended inorganic material, and the quantity of sediment gathered around the roots stands in proportion to the speed of the water current. This deposition of the sediment can amount to more than tenfold the dry weight of the roots (Tab. 3).

Table 2: Differences in weight of the roots at *Paspalum repens* in different localities

I. Running white water rich in suspended material

Locality	Date	Sampling place	Number of root clusters/m²	Dry weight of roots in g/m²	Average dry weight of one root cluster in g
		M[1])	180	20,4	0,11
		M	252	17,6	0,07
		M	148	9,6	0,06
		M	204	7,6	0,04
Costa do Baixio	3. 5. 68	M	176	4,8	0,03
		C[2])	396	27,6	0,07
		C	136	4,0	0,03
		C	336	10,8	0,03
		C	384	5,6	0,01
		C	324	25,6	0,08
		Total amount	2 536	133,6	0,05

II. Settled white-water

Locality	Date	Sampling place	Number of root clusters/m²	Dry weight of roots in g/m²	Average dry weight of one root cluster in g
Lago Calado	6. 7. 68	M	308	88,8	0,29
		C	672	96,0	0,14
	10. 8. 68	M	304	33,2	0,11
		C	868	150,0	0,17
Lago Manacapurú	7. 7. 68	M	176	19,6	0,11
		C	624	72,0	0,12
	11. 8. 68	M	196	18,8	0,10
		C	572	116,0	0,20
Lago Parú	11. 8. 68	M	476	72,8	0,15
		C	920	186,0	0,20
		Total amount	5 116	853,2	0,17

[1]) M = sample from the marginal region of the population
[2]) C = sample from the central region of the population

Nodes that are cut off sink quickly down owing to the weight of the sediments attached to them. It seems quite possible that the plants use these attached substances for additional nutrition. For a sufficient nutrition so voluminous a root-system would not be necessary, as in the case of plants growing in the lakes.

Table 3: Attached sediments in the roots of *Paspalum repens* in running white-water[1])

Weight of roots per cluster in g	attached sediment, g	g sediment/ g roots
0,246	2,172	8,829
0,383	2,865	7,480
0,490	4,152	8,473
0,114	1,132	9,930
0,400	3,047	7,618
0,558	4,013	7,192
0,450	7,724	17,164
0,153	1,532	10,013

[1]) Investigation at Paraná do Xiborena from April to May 1968

On the contrary the plants in the lakes are forced to develop big root bunches, because normally there exist no appreciable current and inorganic suspended material. Thus the supply of nutrients is not of the same extent as in the Amazon itself. The caught voluminous detritus mainly consists of organic material and $Fe(OH)_3$ that has precipitated.

Furthermore, the smaller quantities of roots offer weaker resistance against the current in running white-water, so that the danger of drifting is decreased. In spite of this, bigger quantities of plants are torn off and washed away again and again. As a result the populations do not grow as old and dense as in the lakes (Tab. 4, 5). Concerning the population at the Costa do Baixio — a broad embankment-line with sediments deposited by the Amazon — only until May a somewhat more dense central region could develop. In June even smaller remnants were found, because by thunderstorm and current more than $^3/_4$ of the population had been drifted away.

Table 4: Dry weight of organic substance in the central region of *Paspalum-repens*-population in running white-water

Date	locality	Stems and leaves g/m²	Roots g/m²	Dead material g/m²	Total weight g/m²
		209,0	27,6	118,2	354,8
		106,0	4,0	36,6	146,6
3. 5. 68	Costa do Baixio	294,6	10,8	94,4	354,8
		272,5	5,6	46,0	324,1
		215,3	25,6	88,0	328,9

Table 5: Dry weight of organic substance in the central region of *Paspalum-repens*-populations in várzea-lakes

Date	locality	Stems and leaves g/m²	Roots g/m²	Dead material g/m²	Total weight g/m²
6. 7. 68	Lago Calado	158,1	80,4	42,4	280,9
6. 7. 68		133,7	96,0	170,1	399,8
10. 8. 68		309,9	136,8	132,0	578,7
10. 8. 68		378,6	150,6	112,0	641,2
6. 9. 68		441,0	161,0	185,6	787,6
7. 7. 68	Lago Manaca-purú	406,2	72,4	276,2	754,8
11. 8. 68		364,3	84,2	78,4	526,9
7. 9. 68		335,7	94,6	284,7	715,0
11. 8. 68	Lago Parú	455,8	186,0	132,3	774,1
13. 9. 68	Lago Castanho	630,7	180,2	328,0	1 138,9

The plants often keep their blister-like swelling on the shoots at such locations which are exposed to the current and grow up with undiminished rapidity until the population gets dry (compare p. 483ff.) due to low water. The thin, hard shoots sprouting from 6 to 8 months-old lake-populations are not developed in such thin populations, and decaying ones observed in the central region of old lake-populations could not be registered in the thin populations of running white-water. Normally due to the fluctuations of water level *Paspalum repens* goes through a change of biotope from water to land, this, however, results in an important loss of substance. But obviously it is also possible that populations of this species live merely aquatic, for a long time. At Lago dos Passarinhos, a lake with only slight water level fluctuations, on the island of Correiro, the grass grew up at places where, the whole year round, the depth of water was at least 2 m.

In concluding we may say that *Paspalum repens* is very much adapted to a floating habitat and it grows luxuriantly in the aquatic environment.

b) *Echinochloa polystachya* (H. B. K.) Hitchcock (Fam. Gramineae)

Syn.: *Oplismenus polystachus* H. B. K., *Panicum spectabile* Nees, *Echinochloa spectabilis* Link.

Brazilian name: "Canarana fluvial". After Black (1950) also "Capim de Angola", "Capim de Pernambuco", at Rio Tocantims "Capim capivara", in Peru "Gramalote".

Besides *Paspalum repens*, *Echinochloa polystachya* is the most important species contributing to the development of the floating meadows in the várzea. These two species together represent about 80 to 90% of floating grass in the Amazon and most of the várzea-lakes in the surroundings of Manaus. *Echinochloa polystachya* is also of great importance as cattle fodder in the várzea-region. Many times it is preferred to *Paspalum repens*, for it has lower contents of water (Tab. 6). Black (1950) stated that it is especially liked by the cattle, whereas horses prefer softer species of grasses. Furthermore, he makes mention of reports, stating that the seeds of *Echinochloa polystachya* are used for human food, however, he himself could not observe such utilization. We have not observed either anything like that. According to our observations in 1967 and 1968 more than 90% of the seedlings were destroyed by larvae of a species from the family Cecidomyidae[1]), that is why an utilization for human consumption was just impossible.

[1]) As these larvae themselves were attacked and destroyed, except the Puparia, by a species from the family of Chalcididae, that is why they could not be defined more exactly.

Photo 6: *Paspalum repens* terrestrial form.

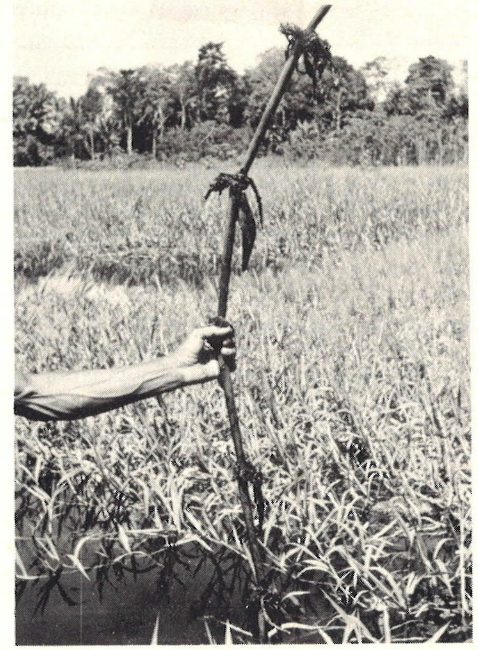

Photo 7: Floating stem of *Echinochloa polystacha* with floating root clusters.

Photo 8: Population of *Echinochloa polystacha* and *Paspalum repens* during the dry period.

Table 6: Difference in water content of the stems of *Echinochloa polystachya*

	waterform	landform
Date	6. 9. 68	2. 3. 68
Total length of stems	348 cm	332 cm
Fresh weight	272,9 g	381,7 g
Dry weight	45,1 g	86,2 g
Water content[1])	83,5%	77,4%
Thickness of stems	1,4—2 cm	

Annual development:

With rising water level the populations of *Echinochloa polystachya* that have survived the dry period, highly increase and the plants grow up vertically, but in contrast to *Paspalum repens* they keep attached to the ground. Just as *Paspalum repens* they develop floating root-clusters at the nodes, which, however, are by far smaller and harder than those of *Paspalum repens* (Photo 7). The main flowering time lasts from April to July. A lot of blossoms are developped, the number of seeds, however, being relatively small, for, as mentioned before, the majority of the seedlings are destroyed by larvae from the family Cecidomyidae. Moreover many birds were seen at the panicles. Black indicates that the seeds are preferably eaten by "marrecas" (different species of the family Anatidae). As proved by laboratory investigations the seeds can germinate after a short time, but in nature the vegetative reproduction is predominant. All young sprouts examined had developed vegetatively from old, partially almost rotten stem-pieces.

After the main flowering time the growth of *Echinochloa polystachya* populations also decreases tremendously, and the plants partially turn yellowish-green. With falling water level the wooden, hard stems cling together more and more densely, forming an entanglement where hardly a boat can get through. Because of the poor developments of roots at the nodes there is a better exchange of water here in contrast to *Paspalum repens*. The temperatures in the central region do not remarkably rise. Furthermore, destruction was not of such an extent as observed in *Paspalum repens*.

When the lake-bottom falls dry, the old stems begin either rotting or take roots in the ground. New sprouts are developed at the nodes and then grow up to big clusters of about 2 m height, and these together with *Paspalum fasciculatum*, form (compare p. 467) a main part of the dry-period-vegetation of the várzea-lake-bottom and the river banks (Photo 8). The difference between land- and waterform is not so striking as that of *Paspalum repens*. The stems, though growing up to more than 20 m in water, do not show striking differences in stem-thickness and leaf-size etc., like those of *Paspalum repens*. Special floating organs like the blister-like swellings of the shoots, as observed in young *Paspalum repens*-plants, are not developed either. The internodes of the plants are filled with aerenchym for floating. There is indeed a difference in water-content, but not so evident as in the case of *Paspalum repens*.

The grass is more dependent on the ground as a substrate. This accounts for the clear zonation which can be observed again and again at the banks of the Amazon and in the lakes. If both species are represented in the same area, there is normally a rather

[1]) See page 461 for note [2])

pure *Echinochloa polystachya*-population growing rooted in the ground near the banks, and the *Paspalum repens*-population is free floating in the deeper water (Fig. 6). It is true that particularly in the Amazon itself the populations are again and again torn off, drifted away and mixed by wind and currents, especially when the grass grows up to 1,5 m above water level, thereby offering a wide surface of impact to the wind. Thus, it results that torn off *Echinochloa polystachya*-populations can exist in any place without contact to the ground for some weeks. When, however, an evident damage is caused, this damage is recognized by the development of fresh, vertically growing sprouts at the nodes of the otherwise not branched stems (Photo 9). The same process was always observed at pieces of stems which were considerably damaged by current, or were partially rotten; they developed similar sprouts in large numbers. In lakes with a relatively constant water level, *Paspalum repens* was found, but not *Echinochloa polystachya* (Lago dos Passarinhos, Lago Jacaretinga, Lago Liuba[1])). The mode of growth points to the fact that this species of grass in its existence directly depends on the fluctuations of water level and needs a dry period for development. Thus *Echinochloa polystachya* cannot be defined as floating grass in the same sense as is *Paspalum repens*.

c) *Paspalum fasciculatum* Willd. (Fam. Gramineae)

Brazilian name: "Murí", "Capim Morí". After Black (1950) in Goiás "Capim do Araguaia", in Mato Grosso "Capim da Praia".

Paspalum fasciculatum is one of the most frequent grasses on the banks of rivers and lakes of the várzea. After Chase (1944) large, almost pure populations also exist at Rio Paraguai and at Rio Apure, an affluent of the Orinoco (Venezuela).

According to Le Cointe (1947) the grass as a fodder plant is of medium value. It is said to give a disagreeable taste to the milk. *Paspalum fasciculatum* has its vegetation period during the low water period. The flowering time at Manaus begins approximately about February. The grass forms dense populations up to 3 m high, so that a machete is necessary to get through.

The wooden, hard stems are firmly anchored in the ground, so that the plants can well resist to currents. In contrast to the other plant species, described here, *Paspalum fasciculatum* does not grow accompanying rising water level, but becomes completely flooded by it. It is not a floating grass, but firmly fastened on the bottom. Smaller floating islands, appearing from time to time, come from slipping bluffs (Braz. "terras caidas") with vegetation on them. During the dry period mixed populations of *Paspalum fasciculatum* and *Echinochloa polystachya* are frequently found. Then with rising water level a separation takes place, because *Echinochloa polystachya* grows up with the water, whereas *Paspalum fasciculatum* is gradually flooded. In case of a coexistence of all the three species, *Paspalum fasciculatum*, *Echinochloa polystachya* and *Paspalum repens* form three zones in the bank regions of rivers and lakes: *Paspalum fasciculatum* rises above water level only near the bank. The population may, however, continue at the bottom up to a depth of 6 to 10 m, subject to the water level. *Echinochloa polystachya*, populating almost the same area, grows up with the water, forming the second zone at the water surface, the stems rooting in the ground among the immersed plants of the *Paspalum fasciculatum*-population. In the front of these the *Paspalum repens*-population forms the third zone, being mostly not in contact with the bottom, and anchors with its tendrils among that of *Echinochloa polystachya*. This "Paspalo-Echinochloetum" can be regarded as a characteristic plant-association for the várzea-region of the medium Amazon.

[1]) The examined lakes will be described in details in the second paper.

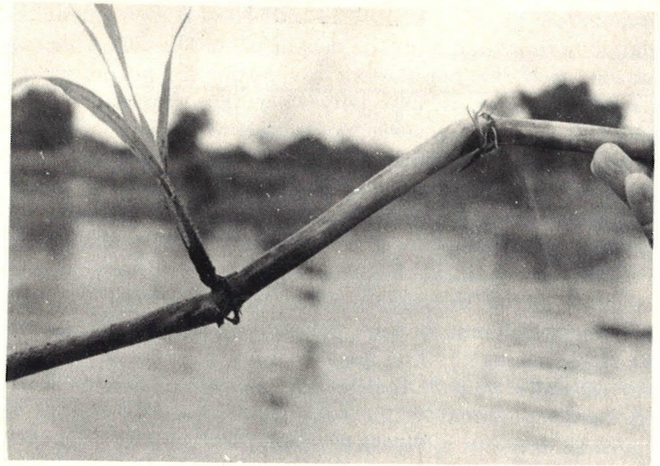

Photo 9: Old stem of *Echinochloa polystacha* damaged by the current with vertically grown new shoot.

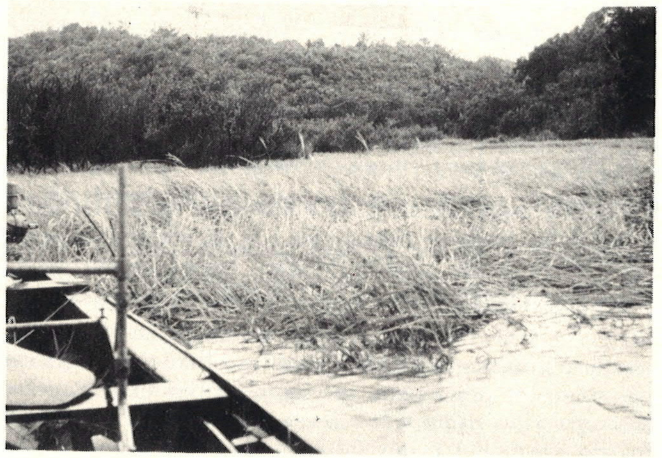

Photo 10: Population of *Oryza perennis* in the marginal region, slightly damaged by the turbulance.

Photo 11: *Victoria regia.*

The danger of being drifted away is of course great for the populations of *Paspalum repens* and also for *Echinochloa polystachya*. *Paspalum fasciculatum* is anchored so firmly that there is hardly any danger of being drifted away. Therefore this grass is of special importance for the stabilization of shores and sedimentary banks. Besides the current is weakened and the sedimentation is enhanced through the dense mass of stems. While describing the populations at Rio Paraguai, CHASE (1944) points out that through the sedimentation-enhancing effect an area of some thousand square kilometers is changed first into marshy land and then, with the immigration of other plant species, into dry land (compare p. 479).

d) *Leersia hexandra* SWART (Fam. Gramineae)

Brazilian name: "Cenéuáua", "Capim peripomongo", "Andrequicé", "Arroz bravo", "Arroz de Caiena".

Leersia hexandra is spread over the whole tropical region of South America (BLACK 1950). In Amazonia the distribution-area reaches from the foot of the Andes until the mouth of the Amazon. In Trinidad as well as on Marajó (the large island in the Amazon-mouth), this species lives in shallow lakes, which are surrounded by *Montrichardia arborescens* SCHOTT (Fam. Araceae), *Gynerium sagittatum* BEAUV. (Fam. Gramineae) and *Cyperus giganteus* VAHL (Fam. Cyperaceae). According to MIRANDA (1907) *Leersia hexandra* especially populates the "Mondongos" on Marajó, which are muddy, humid depressions. Other large populations are described by BLACK (1950) in the várzea of Rio Cupari. Occasionally this species happens to appear in mixed populations with other grasses. Near Santarém BLACK found these among *Paspalum repens*. According to BLACK the extensive distribution of *Leersia hexandra* in Trinidad has been accelerated by the fire which destroys the inundation forest and thus facilitates its advance. LE COINTE states that it is susceptible to fire and destruction by footsteps of cattle. In spite of the sharp edged leaves *Leersia hexandra* is considered as one of the most valuable floating fodder plants.

In the surroundings of Manaus more important populations of this species were primarily found in lakes where the water level showed little fluctuation (Lago dos Passarinhos, Lago Jacaretinga[1])), or at places which remained humid even during low water level (some bays of Lago do Rei, Lago Castanho, Lago Parú[1])). Evident differences between land- and waterforms, such as found in *Paspalum repens* could not be observed. It was very often the case in lakes with a relatively constant water level that one part of the population was normally terrestial or paludal, whilst the other was floating for years or even always at the water surface (Lago dos Passarinhos). In 1967/68 the water level of Lago Jacaretinga had reached its low point and the part of the population having grown above the water level for more than 1 to 1,5 m died away. All these observations indicate that *Leersia hexandra* is susceptible to dryness. This seems to be reason why no floating populations were observed on the banks of the Solimões-Amazon. Because of the considerable annual water level fluctuations they dry up too much during low water period. Single islands, drifting down the river at high water level, probably originate from lakes.

The dead stems of *Leersia hexandra* do not decay in water as quickly as those of *Paspalum repens*. This may probably be explained by the remarkably lower water content (Tab. 7). A new generation of *Paspalum repens* does not find good conditions essential for life at the same place before the preceding one has decayed and there is sufficient room for the

[1]) The lakes examined will be described more exactly in a second paper.

new plants for their development, whereas the new generation of *Leersia hexandra* populates the dead layers of old stems and roots. In the course of time thus a dense floating cushion develops, growing up to a thickness of 50 cm and more. The rhizomes and stems of one generation are very closely interlaced to each other and form a cushion of horizontal layers (Fig. 7). In Lago dos Passarinhos a pure population could be divided into a maximum of 6 such layers. The first 3 layers had already decayed to a large extent and their lines of separation had almost gone. They were partially loosened in pieces from the underside of the cushion, so that a state of equilibrium was attained between composition in the vivid and decomposition in the dead part of the population and the maximum density of the cushion was thus attained.

Table 7: Water content of the stems of *Paspalum repens* and *Leersia hexandra* in floating populations

Plant species	Paspalum repens, Waterform young	Leersia hexandra Waterform old	
Date	6. 2. 68	6. 9. 68	6. 9. 68
Fresh weight/g	54,3	175,0	23,9
Dry weight	2,5	8,7	8,7
Water content %[1])	95,4	85,2	63,6

e) *Hymenachne amplexicaulis* (Rudge) Nees (Fam. Gramineae)

Brazilian name: "Canarana de fôlha miuda", "Rabo de raposa", "Capim camalote da água".

According to Miranda (1907) and Le Cointe (1947) *Hymenachne amplexicaulis* contributes very much to the formation of floating islands in the Amazon. Black (1950) describes large populations in the lakes of Rio Cuparí. According to Le Cointe this grass is especially valuable for cattle as a fodder plant. In the surroundings of Manaus we found only a few large populations of this species at the Costa do Baixio among *Echinochloa polystachya*. Both species seem to prefer the same biotope. On a trip to Santarém in June 1968 more important large populations, which had taken the place of *Echinochloa polystachya* populations were found in some backwaters of the Amazon. In contrast to the statement made by Miranda and Le Cointe this grass does not contribute to the formation of large floating islands near Manaus.

f) *Panicum chloroticum* Nees (Fam. Gramineae)

Neither Le Cointe nor Miranda mention this species. Black (1950) observed this species in small number in the lower Amazon, further he mentions that it was observed by J. M. Pires in the upper Solimões.

Around Manaus in Lago Calado, at Costa do Baixio and at Paraná do Xiborena *Panicum chloroticum* existed sporadically. In Lago Calado this species formed a mixed population together with *Oryza perennis*. *Panicum chloroticum* disappeared with rising water about the end of March in all locations.

g) *Oryza perennis* Moench. (Fam. Gramineae)

At the time of investigations in Lago Calado and Lago Manacapurú important populations of this species were found. They grew up with rising water, the stems getting longer than 3 m. The plants kept on fastened to the bottom at places protected from the wind. They were soon torn off and drifted at the surface at locations exposed to the

[1]) See page 461 for note [2])

wind (Photo 10). This species does not seem to be highly adapted to a floating habitat, because the torn off plants soon get rotten, although small root-clusters are developed at the nodes. Le Cointe mentions that Oryza species also contribute to the formation of the floating islands; in that case, however, it must have been only those plants which were torn off and drifted away. In the Amazon River *Oryza perennis* was only found sporadically at places which were protected from the current. In lakes with little fluctuation in the water level this species was not found. This may probably be due to the germination by seeds at the lake bottom and therefore to a dependency on a period of low water.

Cattle like to feed especially on young populations, therefore the animals often go into the water. Le Cointe does not mention this species, but observed a related species (*Oryza subulata* Nees.), which has a high fodder value until its ripeness, afterwards, however, it may become dangerous for the cattle because of the awns of the seeds.

h) Family Cyperaceae

Some species of the Family of Cyperaceae[1]) require biotopic conditions similar to those of *Leersia hexandra*. They shall be treated here altogether. The most important species in the lakes examined by us was *Scirpus cubensis* Poepp Kunth., and it was also found by Marlier (1965) in Lago Redondo, a lake at the Ilha do Careiro. Many times this species was found in large pure populations where *Leersia hexandra* was also present in large quantities. The strong root-system and the hard rhizomes lead to the formation of dense floating cushions. The process of decay goes on rather slowly — as it does in the case of *Leersia hexandra* — so that older populations of these species also grow up on their own dead remainders.

i) Other floating plants

The most common species are:

Eichhornia crassipes Mart., (Fam. Pontederiaceae)
Reussia rotundifolia L. (Fam. Pontederiaceae)
Neptunia oleracea Lour. (Fam. Leguminosae)
Phyllanthus fluitans (Fam. Euphorbiaceae)
Jussiaea natans Hum. Bonpl. (Fam. Onagraceae)
Pistia stratiotes Linn. (Fam. Araceae)
Ceratopteris spec. (Fam. Parceriaceae)
Salvinia auriculata Aubiet (Fam. Salviniaceae)
Azolla spec. (Fam. Salviniaceae)
Marsilia spec. (Fam. Marsiliaceae)

Optimal conditions of development for the smaller species are especially found in the calm bays of the várzea-lakes which are protected from winds and currents. It happens, however, again and again that parts of the populations are drifted into the Amazon River where they are attached to clods of floating grasses. Only the large and robust species such as *Pistia stratiotes*, *Eichhornia crassipes* and *Reussia rotundifolia* find conditions essential to them near the banks of the Amazon River.

[1]) The material collected is being worked on in Brazil.

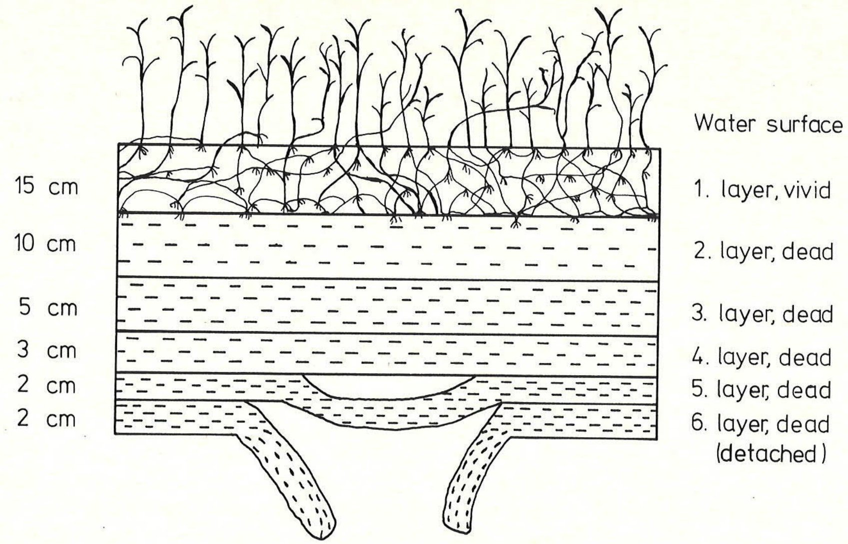

Fig. 7: Schematic cross-section through a pure Leersia hexandra-population

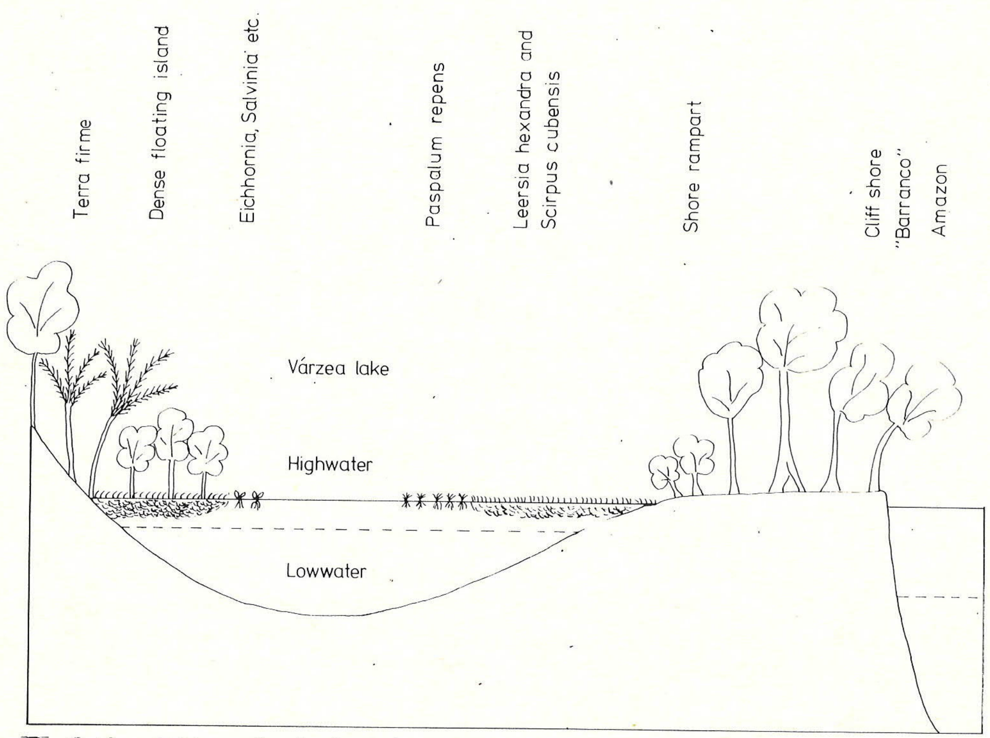

Fig. 8: Vegetation of a typical Várzea lake with small oscillations of water-level (Schematic)

During low water level the floating plant populations can grow unmolested, especially in secluded lagoons. During the dry period of 1967/68 *Pistia stratiotes* showed an evidently high growth in Lago do Xiborena, a várzea-lake covering some hectars near the Rio Negro-mouth. As soon as with rising water the connection with the Amazon was re-established, the main part of the population was drifted into the river.

Obviously at the same time in other lakes as well a high increase of *Pistia stratiotes* had taken place, for in January enourmous masses of it driftet down the Amazon. At a place protected from currents vis-á-vis the Rio Negro-mouth the plants got concentrated in large quantities and covered the river for kilometers. During the rest of the year so big quantities of plants could not be observed again.

With rising water level a high development, primarily of *Salvinia auriculata* and *Azolla sp.*, began in the calm lake bays (Lago do Xiborena, Lago Calado, Lago de Manacapurú); it was probably caused by the influx of fresh Amazon water. However, two months later, the large quantities drifted away and the populations were reduced to their normal size. Compared to the semiaquatic Gramineae and Cyperaceae these plants were not so important with regard to the production of organic material. Among the species registered *Victoria regia* Lindbl. (Fam. Nymphaceae) is also found down to depth of water of 8—10 m. It is always an impressing view for an onlooker to see a secluded lake bay covered some times with hundreds of the huge leaves of this plant (Photo 11).

Utricularia sp. (Fam. Lentibulariaceae) was the only submerged plant in the surroundings of Manaus. In Lago Calado and Lago Manacapurú it appeared as early as in January, soon after the beginning of the rising water level, but during the whole period of investigation it was not observed in large quantities.

It is a striking fact that *Eichhornia crassipes* does not develop in masses in the Amazon region, whereas in other tropical regions it can completely cover even vast water areas within a short time, and may become a real pest (Berg 1961, Bard 1965, van Donselaar 1963—1969 a. o.). The reason why it is not found in great numbers in the Amazon, can probably be attributed to a large number of biotic and abiotic regulating factors in its original distribution area. Biotic factors are attack of parasites (Bennett and Zwölfer 1968) and a keen competition with other floating plants, especially the one with floating Gramineae. The abiotic mechanisms of regulation are represented by the nutrient-contents of the waters, the continuous drifting by the current and above all by the high water level fluctuations, which annually destroy more than 90% of the floating populations. If this complicated balance does not exist — for instance in areas where the plant did not exist before, but was introduced or accidently brought in — or if this balance is disturbed, a development in masses may occur (Botsch 1970). These mass developments are in any case the indicators for a deeply disturbed natural balance.

IV. "Secondary colonization" of floating populations with Macrophytes

The floating vegetation has opened an area of hundreds of square-kilometers as a new space required for life, in the lakes of the várzea-region as well as in the Amazon itself. This, however, does not put an end to the development. The floating plant masses on their part represent another specific biotope that can be "secondarily" settled by non-floating species.

Life time, type and density of the floating substrate are of decisive importance for a colonization by non-floating plants. These depend on the biotope, the species of plants that form the floating population, and their age. Young stocks are generally lighter than

older ones, because only in the course of time the greatest possible density of population will be reached. Besides, the part of dead pieces of plants increases until the balance between decrease and increase of substance will be reached. Corresponding to that it may be said that up to a certain degree the density of floating cushions increases with their age.

If we regard the above described plants under these aspects, the following three groups can be registered:

1. populations existing only for few days or weeks
2. populations existing for several months
3. populations existing for several years or decades.

Group 1 is formed by *Eichhornia crassipes*, *Salvinia auriculata*, *Azolla sp.*, etc. Though being able to cover larg water areas, these species do not offer an everlasting space for colonization to "secondary colonizers", for they are not closely bound to each other and thus can be torn off and drifted away by wind and current after a short time. A "secondary colonization" by macrophytes does not take place in this case.

Group 2 is primarily formed by *Paspalum repens* and *Echinochloa polystachya*.

A "secondary colonization" takes place to a small extent, generally limited to one year, and include often climbing species. Repercussions on the primary populations are normally not found.

Group 3 consists of *Leersia hexandra* and all sorts of floating species of the Family Cyperaceae.

In this case also perennial plants growing more slowly have time enough for colonization. Besides, when settling, they find a relatively compact medium for an easy rooting.

Just by the root system of the perennial newly imported species the floating cushion is kept together more densely. Leaf-fall makes it more and more solid, and in the course of time a sort of soil-formation takes place. This on the other hand allows a colonization to other terrestrial species. In the meantime the conditions of the biotope have so much deteriorated, that the first colonizers have mostly been extinguished and at times can only be found in the marginal regions, where they gradually enlarge the floating island. The newly developed community of plants, however, keeps its biotope for itself. The age of such cushions may be indicated by their thickness and the vegetation growing on them. In Lago Parú a floating island which had grown to a thickness of more than 1 m (Photo 12, 13) was examined. The lower margin could not be studied with certainty. The density was comparable to that of peat. Besides various grasses and ferns, the island was also covered with *Cecropia sp.* (Fam. Moraceae) and *Cassia grandis* L.F. (Fam.Leguminosae). On other islands *Bombax munguba* MORT., (Fam. Bombaceae) and *Montrichardia arborescens* SCHOTT (Fam. Araceae) were found. According to reports of local inhabitants these islands on the lakes are drifted away by the wind. At a lower water level they remain on the dry lake-bottom for a long time. With rising water level, however, they begin again to float. At times they can be a real handicap to navigation, when i. e. closing the connection of the lakes with the Amazon. Sometimes during the dry season they are burnt by the inhabitants, and during high water level are sawn to pieces and hauled by boats into the Amazon, where the plant masses are drifted away by the current.

As a rule it is very difficult for other species to gain a foothold in a biotope that is already densely populated by another species. Thus, the appearance of larger floating areas of *Leersia hexandra* or of *Scirpus cubensis*, does not necessarily lead to a "secondary

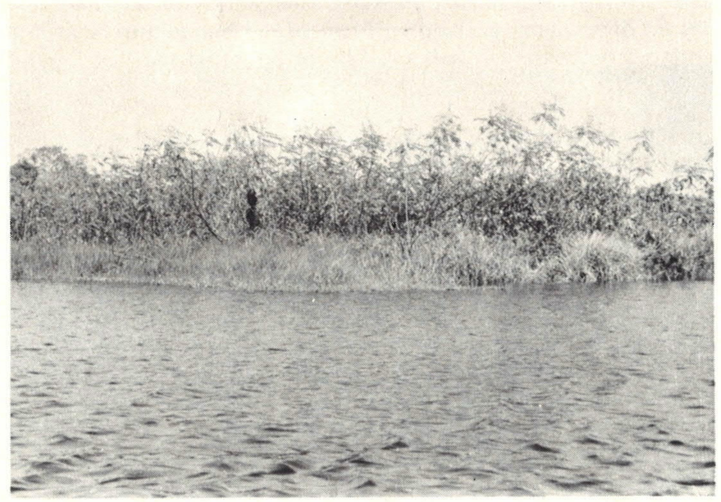

Photo 12: Floating island with "secondary population". On the marginal region exist the primary species: *Leersia hexandra* and *Cyperus spec.* (Lago Parú).

Photo 13: Central region of the floating island.

Photo 14: Mechanical damage to *Paspalum repens* in the current region of the Amazon.

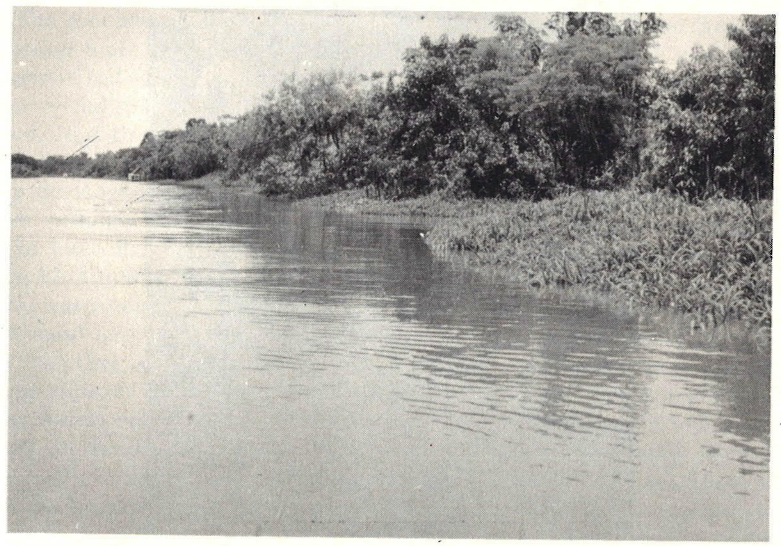

Photo 15: Small *Paspalum repens* population (Paraná do Xiborena).

colonization" with the above described consequences. This is proved by large pure populations of these species and by the fact that floating islands with an extreme "secondary population" will not be found in all lakes that are qualified for the formations of such islands.

V. Subdivision of the várzea waters into biotopes

As far as the floating vegetation is concerned, the waters of the várzea regions can be subdivided into different biotopes. Each of these biotopes is created and limited by factors which fundamentally influence the existence, the composition of various species, and the development of the floating vegetation. From ecological studies made on a single species of plants in the preceding chapters, a conclusion will be drawn on these biotopes in general.

A. Current region of the Amazon
(Free water area)
Biotope-forming factors:

a) strong currents and strong undulations
b) deep water
c) high quantities of fine, suspended, inorganic material, and small degree of transparency (about 30 to 40 cm)
d) homothermal layer of water
e) relatively constant pH-value (about 6,8)
relatively high electrical conductivity values (about 60 μS_{20})[1])

B. Bank- and sedimentation zones in the Amazon
Biotope-forming factors:

a) weak current
b) shallow water; dry at low water level
c) variable land-water-limitation in respect to water level
d) great quantities of fine, suspended inorganic material and low transparency
e) homothermal layer
f) relatively constant pH-value (about 6,8)
relatively high electrical conductivity values (about 60 μS_{20})

C. Várzea lakes with high fluctuactions in water level
(with continuous connection to the main river)
Biotope-forming factors:

a) normally no current
b) shallow water; during dry period noticeable fall of water level; mainly dry
c) only sometimes turbid by inorganic suspended material and normally good transparency (80 to 200 cm)[2])
d) temperature stratifications with normally diurnal changes
e) changing pH-value, changing content of electrolytes[2])

---

[1]) Further detailed investigations on the chemistry of Solimões-Amazonas and várzea lakes are being concluded by Schmidt in Manaus.

[2]) Measured values are given in the description of biotopes in the second paper along with the nvestigation of aquatic animals.

D. Várzea lakes with relatively small fluctuations in water level (connection with main river only at the time of highest water level)
Biotope-forming factors:

a) no current

b) shallow water, in dry time only slightly falling water level.
The other factors as in C, above.

VI. The aquatic and semiaquatic vegetations of the biotopes mentioned

a) The vegetation of the current-region

The determining factors for settlement in the current region of the Amazon are the strong current and the undulation. The current very quickly carries the drifting vegetation away. If we take into account, that from other biotopes, new plants are continuatly drifted into the river, the current region may be regarded as a biotope of its own in so far as it keeps the drifting plants alive because of the relatively good conditions of nutrients and light, so that their growth may even be advanced. But in the long run the considerable water-movement has rather a negative effect on the drifting populations. Because of the continual mechanical strain, caused by the waves, stems and roots are injured and the plants get completely flooded in the course of time (Photo 14). Exclusively robust floating forms like *Eichhornia, Reussia* and *Pistia* can tolerate this strain longer. However, mechanically injured plants were found again and again in this region.

Under these circumstances the current region of the Amazon is to be regarded as a biotope that cannot be permanently occupied by vegetation. The living plants which are drifted in from other biotopes will sooner or later be destroyed by the considerable water movement, if not drifted away by wind or current into more favourable biotopes.

The dependency of the current-region on the other biotopes is accentuated by the fact that during the low water period, beginning about October and lasting until December, no or only small quantities of floating vegetation are found in the river. Only with rising water level, when the connection with the isolated waters is re-established, bigger quantities of floating plants appear in the river.

The characteristic succession of species can therefore easily be explained by their ecological requirements. Shortly after the beginning of rising water level, about January, mainly plants not forming compact masses, get out into the main stream, (in 1968 *Pistia stratiotes* was first and foremost).

These species have increased undisturbed in isolated waters, which were cut off from the main stream for some time. As soon as the water level rises the connection is re-established, and they are drifted into the main stream. The influx of fresh white-water into the lakes increases the ratio of growth of the remaining plants, so that with the rising water level — about the beginning of March — comparatively many plants, which are not forming compact masses, can appear in the current region. Especially, *Paspalum repens* can appear at the same time in small masses, for this species can also survive floating in isolated waters. At the beginning of a rising water level, however, the connections of the lakes with the Amazon are generally very narrow. Therefore the compact masses of *Paspalum repens* are generally kept back. At a further rise of the water level the mouths of the lakes widen and parts of the populations highly increased by then are drifted into the main stream. During this period a considerable increase of vegetation sets in on the banks as well. After a few week the quantity of *Paspalum repens* surpasses

that of the other floating plants within the current region. At that time *Echinochloa polystachya* does not yet appear, as the growing up populations are still fastened to the bottom. Only about April more and more islands of *Echinochloa polystachya* appear because current increases with rising water level in the bank-regions, and carries off parts of the populations. The violent thunderstorms setting in about May also partially loosen the plants in the lakes from the bottom and drift them away, so that from that time on, more than 90% of the vegetation drifting down the river is composed of almost equal quantities of *Paspalum repens* and *Echinochloa polystachya*. At sinking water level the water of the lakes carrying large amounts of floating islands runs back into the river. In the course of time larger and larger areas of the lake bottom fall dry, on which the populations remain, so that in 1967 from October until December only very little floating vegetation was found in the main stream. As the Amazon does not rise and fall equally every year (Fig. 2), the appearance of the diverse species can vary even by months.

b) The vegetation of the bank- and sedimentation-regions

The bank- and sedimentation-regions in the Amazon represent a biotope which may have a size of many hundred square-kilometers. The decisive factors for the population of this biotope must be seen in the changing water-land-limitation, and this is mostly related to the diminution of currents.

At places protected from currents, the river deposits sediments on areas of often several square-kilometers. In the course of time the river-bed thereby becomes more and more shallow, until finally at dry periods large sedimentary banks emerge from the water. Then the colonization starts mainly by *Echinochloa polystachya, Paspalum repens* and *Hymenachne amplexicaulis, Paspalum fasciculatum* advancing more and more from the banks. *Salix humboldtiana* WILLD. (Fam. Salicaceae) settles down as the first tree in the highest places. With rising water an explosionlike development of vegetation sets in. The plants grow up with the water and form huge "floating meadows".

The strong thunderstorms, generally in May, however, loosen considerable parts of the populations and drift them away. Here *Paspalum repens* is especially concerned, as mentioned before, because it forms the zone which is often totally carried away into the river.

The same conditions apply to the small shore-lines (Photo 15). But there the protected sector is only a few meters broad and the populations are frequently torn off. Nevertheless generally a new colonization takes place.

This may happen through plants carried there by currents. In this case *Paspalum repens* is predominating. The colonization may also have started from the landside namely by populations, which were not inundated before, but afterwards were flooded and finally begin to grow with rapidity. This is particularly the case for *Echinochloa polystachya*. The dynamic in this area is shown by *Paspalum repens* populations, for they permanently keep the appearance of young plants (compare p. 483). An exception, however, are the bluffs where the river strongly erodes. Here, the watermovement is so intensive and the erosion of banks is so quick, that a colonization is hardly possible. During dry period here and there the sedimentation-zones and shore-lines are used for agricultural purposes by the inhabitants. In addition to this there are also large jute-plantations (*Corchorus capsularis* L., Fam. Tiliaceae). For this purpose the original vegetation, consisting mainly of *Paspalum fasciculatum* and *Echinochloa polystachya*, is cleared off. These areas are especially fertile, for every year the river deposits a layer of fresh sediments. The sedimentation is supported by the semiaquatic plantpopulations, which reduce the current, keep the suspended material with their entanglement of stems and

roots (compare p. 469) and protect the banks from erosion. Thus autochthonous populations, mainly of *Paspalum fasciculatum* and *Echinochloa polystachya* can be regarded as indicators of areas for agricultural utilization. *Paspalum repens* turns out to be a less good indicator, as there is no direct connection with the ground which is primarily due to the floating habitat of this species. In order to get an optimal utilization of these areas, however, it would be indispensable to measure regularly the water levels in the bigger affluents and in the upper course of the Solimões-Amazon so as to be able to predict the rising water level some weeks before, because on this last consequence the agronomically utilizable area is dependent. The lack of such a prediction also in view of the actually extensive utilization of these areas can lead to partially important losses in yield and to an inferior quality of products, especially when jute is being cultivated

c) The vegetation of várzea-lakes with high fluctuations in water level

These lakes represent the most important biotope with regard to biological production. Furthermore they are also the richest in species. All lakes of this kind contain — except at periods of low water level-large populations of *Paspalum repens* and *Echinochloa polystachya* (Photo 16). From many places at the shore *Paspalum fasciculatum* advances to the interior of the lake. In some lakes populations of *Oryza*-species, *Hymenachne amplexicaulis* and *Panicum chloroticum* grow up with rising water. In waters isolated from the rivers, and especially at rising water level, there is a high increase of *Eichhornia*, *Reussia*, *Pistia*, *Salvinia*, etc. Furthermore, we find there *Utricularia spec.*, at times great populations of *Victoria regia*, diverse floating species of the family Cyperaceae and *Leersia hexandra*.

The whole year round more or less large parts of the populations are drifted from the lakes into the Amazon. This happens especially when water from the lakes flows into the Amazon, thus causing a slight current within the area of the lake-mouth in the direction to the Amazon. This can be brought about by different factors, e. g. by falling of the river level, by Amazon water streaming in to the lake above its mouth, by intensive local rainfalls over the lake or in its drainage area or by strong influx from terra-firme-creeks. Another important factor is drifting caused by wind. Generally, however, the inhabitants consider the appearance of an especially great number of floating vegetation in the Amazon as a sign for stagnation or falling of the river level.

In spite of the high production of organic matter in the várzea-lakes, there are usually no organogene symptoms of land formation observed, not to that extent any way as this phenomenon occurs for example in European waters. Hueck (1966) refers this to the fact that there is no zone of reed-plants in the Amazon — with the exception of *Montrichardia arborescens* Schott (Fam. Araceae) — which develop their roots in the lake-bottom. Our observations seem to be contrary to Hueck's (1966) statement, as we have found e. g. two important species — *Echinochloa polystachya* and *Paspalum fasciculatum* — which are perennially rooted in large parts of the lake-bottom. During the highest water level the roots go down to more than 8 m below the water level, a depth where European reed-plants cannot exist. In our opinion it is almost sure that the quick remineralization of the organic matter, which is caused by high temperatures, and the lake-bottom falling periodically dry is the reason why no symptoms of land formation are normally found. On the other hand it must be pointed out that at periods of falling water level of the Amazon not only inorganic suspended material, but also great quantities of organic detritus can be washed out of the lakes, it might either be in the form of floating islands or in form of small particles. As the Amazon often falls more than 20 cm per day, the lake water frequently runs out of the narrow lake-mouths at a velocity of more than 1 m/sec. The waters soon become so shallow that turbulences caused by

wind whirl up the lake-bottom, the degree of transparency dropping to less than 20 cm. In October 1967 the water running out of Lago Calado had a transparency of less than 10 cm. In order to make the phenomenon of land formation understandable, a detailed investigation would be necessary regarding the balance in the lakes between material imported and exported. In comparison to the land formation in some European lakes by "Schwingrasen" the land formation in várzea lakes is brought about by perennial thick floating islands, which are exclusively built up by the floating vegetation.

d) The vegetation of várzea-lakes with relatively small fluctuations in water level

Compared to the main river the most important characteristic of these lakes is the little fluctuation in water level. This biotope is especially qualified for the development of large, often relatively old populations of *Leersia hexandra* and diverse floating species of the family Cyperaceae (Fig. 8), whose importance for the organogene processes of land formation has already been mentioned. *Paspalum repens*, as well as *Victoria regia*, *Azolla*, *Eichhornia* etc. are found there. *Echinochloa polystachya*, *Paspalum fasciculatum* and *Hymenachne amplexicaulis* are nearly almost receding or completely lacking, as their good development is dependent on an annual dry period of the biotope.

e) The influence of black-water on the vegetation

According to Gessner (1959) the existence of semiaquatic Gramineae makes it possible to state exactly how far the influence of black-water can reach, as these do not exist in it; according to our observations it, however, can be stated that these plants do exist as far as there may be an influence of white-water. Obviously the aquatic and semiaquatic vegetations are actually capable of existing in black-water, for a few months, and can grow as well, on condition that every now and then the water should become richer in electrolytes and less acidic. Within the mouth-region of Rio Negro (i. e. Lago Janauarí) we found very large populations of *Paspalum repens* and *Echinochloa polystachya* in predominant black-water, and the same was valid for Manacapurú. In pure black-water we did not observe any autochthonous populations of the above mentioned vegetation. More detailed investigation, however, was only made in the lower course of Rio Negro. Every now and the then populations appearing near Manaus were due to drifting by wind or current from other biotopes.

More detailed investigations regarding the influence of black-water on the distribution of *Eichhornia crassipes* Mart. was carried out by Berg (1961) in the Congo region. He found out that the pH-value was the limitating factor for the distribution of plants. In waters with a pH-value below 4,2 *Eichhornia crassipes* was absent. We need not point out that there are no fixed transitions between the described biotope and the colonizing vegetation. Furthermore, this is even favoured by the considerable water level fluctuations which make the transitions between biotopes more variable.

VII. Primary production of *Paspalum repens* Berg

As we may conclude from the preceding chapters, the floating plant populations are of great importance for primary production of the várzea-waters. First quantitative data can be found in Marlier (1965). For Lago Redondo he reported a production-surplus of 1.000 g dry weight/m^2/2$^1/_2$ months. Considering that this efficiency of production is lasting for the whole year, he calculated a net production of 50 t/ha/annum;

he mentioned, however, that this figure should be regarded with discretion because of the method used. This estimation obviously refers to the whole floating vegetation of Lago Redondo where *Paspalum repens*, after MARLIER (1962), represents the main element of its flora.

Quantitative investigations of *Paspalum repens*-populations from biotopes investigated by us show that the estimation of production mentioned above seems too high for the following reasons. The grass is able to cover quickly large water areas with a dense plant-layer, this, however, can only reach a certain maximum thickness. According to our measurements in the várzea-lakes the quantity of stems in the central region of the older populations amounts to about 100 m/m². Only in one case the quantity was greater. Including the roots, leaves and dead plant-pieces the dry weight was about 600 to 800 g per m² or 6 to 8 t/ha (Tab. 5, p. 21). This density is reached within nearly a 6 months' period, afterwards, however, it does not considerably increase, since during the main flowering period the growth in the central region of the population is to large extent stopped. An increase takes place only in the marginal region, which is not so dense anyway. The period without any noticeable increase comprehends several months. Afterwards the populations die and get rotten or get stuck on the tree-tops and dry up during low water level. During the rotting period the newly developed hard, thin sprouts do not produce any important quantities of organic substance, so that only after the disappearance of the old population the primary production can start again to such an amount as mentioned previously in the text. In the várzea-lakes with particularly high fluctuations of water level this development goes on according to the rhythm of high and low water.

According to MARLIER's hydrographical data Lago Redondo is connected only for a short period with the Amazon, and shows no distinct decrease in water level. Therefore it is possible that populations of different age groups can exist simultaneously, and make the impression that the productivity of the plants is of an equal level during the whole year. But in reality this is not the case, because it depends, as mentioned before, on the age and the state of development of the population, so that the real production surplus is by far less than calculated by MARLIER.

Furthermore, the calculation of the real quantity of substance must be taken into account, because the *Paspalum repens*-populations are not so dense in the marginal regions and there are great variations in the densities in the central regions (Tab. 5, p. 464). According to our estimations the extent of the marginal region can considerably vary, but it is normally between 2 and 3 m. We can only take into account about 50% of the plant mass of the central region. If the above mentioned facts are not taken into consideration for the various forms of floating populations and the population area is simply multiplied with the maximum density of natural populations, this might lead to values that undoubtedly are far beyond the real quantity of organic substance. According to our cautious estimations the production-surplus of large populations amounts to 6—8 t of dry substance per hectar per high water period in várzea-lakes with considerably fluctuating level. The decay is accelerated by old populations falling dry, and every year a new generation can develop under optimal conditions. This is not the case in lakes without great water level fluctuations, so the production rate of these populations should be somewhat lower. In the large sedimentation-areas of the Amazon, i. e. Costa do Baixio, where according to our experience populations get less old and dense because of the hydrographical conditions, a real production-surplus of 3—5 t/ha can be assumed. Even lower values of production are to be expected from the thin populations which — because of the currents — exist within the range of a few meters from the Amazon bank

only for a short period. These figures, as mentioned above, only represent the developed quantity of organic substance produced per unit time and unit area. This does not, however, actually reflect the dynamic in which the growth of *Paspalum repens* gets on, as the quantity of the population-forming seeds or plants is not known. In order to study this, a floating square wire-net-box of 150 × 150 cm, and 100 cm high with the upper side open was fixed at the Costa do Baixio. This box dipped in water to a depth of 50 cm. On 14th April 1968, 10 pieces of *Paspalum repens*-stems were planted in with about $^1/_2$ to 1 m length. Simultaneously the same quantity of stems were dried and weighed. The weight was 39,3 g. On 3rd May 1968 the planted stems were harvested and dried. They weighed 220 g. This means an increase in weight of 460% within 19 days (= 24,2% per day).

As just mentioned, this data is just a clue, for it only shows a short period within the entire development of single plants. Due to the experimental conditions, there might be mistakes, as the natural conditions were partially disturbed (e. g. it is possible that too short pieces of stems were planted). Information about the individual development of *Paspalum repens* will first be given by complete curves of growth of the single plants under different biotope conditions.

There is a relation between individual development and population development, the latter being of great importance for the production of organic substance. Investigations on this complex of questions will be treated in the following chapter.

Here it must be especially pointed out that in investigations on the growth of floating populations, formed by several generations, it is easily possible that methodical mistakes should occur for *Leersia hexandra* and the diverse floating species of the family Cyperaceae. These plants grow on their own dead material whose age can only be determined with difficulty, therefore the real increase per unit time cannot be exactly calculated. In Lago dos Passarinhos e. g., in an older exclusively *Leersia hexandra*-population the total quantity of organic dry substance was 2500 g/m². For the above mentioned reasons this figure, however, only indicates the given quantity of floating material and does not show any real values of productivity of *Leersia hexandra*.

In comparison to the productivity of *Paspalum repens* some values for marsh plants are calculated here. The indicated weights refer to the surface dry mass/ha/annum. Possible data about the total dry weight are given, and sampling place and author are also mentioned (Tab. 8). The data are taken from a summary by LIETH (1962).

VIII. Investigations on the population development of *Paspalum repens* BERG in different biotopes

As described above (p. 456 ff.), a *Paspalum repens*-population, when allowed to develop without the influence of currents, first goes through an exponential phase of growth for 4—6 months until the beginning of the main flowering period around June. During this time it approaches a certain maximum density in its central region, which results from the total quantity of organic matter per unit area. After the blossom period the growth largely stagnates. Then it only increases in the marginal region. According to the hydrographical conditions the population decays floating or falls dry.

The growth intensity of the plants is among others related to the quantity of activity of leaves and shoots. As the leaves of *Paspalum repens* are only active when they are near the shoots, and die when they are farther away (about 50 cm), it must be possible to draw conclusions from the relation between the number of shoots and the total quantity of stems per unit of area on the intensity of growth of the population.

Table 8: Productivity of marsh plants (after LIETH 1962)

Plant species	Weight (t/ha/annum)	Locality	Author and year
Phragmites	26,9	Long Island N. York/USA	HARPER 1918
Phragmites	20,6 2,2	Roudsea/E.	GORHAM, PEARSALL 1956
Phragmites	25,0 10,6 7,55 13,0 10,7	Esthwaite/E.	GORHAM, PEARSALL 1956
Typha latifolia, *Typha angustifolia*	14,0	Cedar Creek/ Minnesota/USA	BRAY 1960
Carex lasiocarpa	4,8	Cedar Creek/ Minnesota/USA	BRAY 1960
Carex acutiformis	6,3	Mansergh/E.	PEARSALL, GORHAM 1956
Carex arenaria	4,0	Lakenheath/E.	PEARSALL, GORHAM 1956
Carex lasiocarpa	5,1	Dale Park, Kinara	PEARSALL, GORHAM 1956
Carex rostrata	4,2	Kinara, Mansergh, Wise Een/E.	PEARSALL, GORHAM 1956
Juncus effusus	8,0	Clougha/E.	PEARSALL, GORHAM 1956
Juncus squarrosus	6,9	Clougha/E.	PEARSALL, GORHAM 1956
Zizania aquatica	5,8 (6,3)	Cedar Creek/ Minnesota/USA	BRAY, LAWRENCE, PEARSON 1959
Equisetum fluviatile . . .	3,2	Cedar Creek/ Minnesota/USA	BRAY 1960
Phalaris	8,7	Esthwaite/E.	PEARSALL, GORHAM 1956
Nymphaea odorata . . .	1,1	Cedar Creek/ Minnesota/USA	BRAY 1960

Besides, at an advancing age, the number of shoots — in relation to the quantity of stems — is always much reduced by attack of parasites. Likewise a reduction is caused by the formation of flowers, as the shoot which forms the blossom, dries up at the ripening of the seed. Therefore the relation between the quantity of stems — this is given in length of stems — and the number of shoots must also allow a determination of the age of the population. This will be checked on four populations which grew up in different biotopes.

Population A

In 1968 this population developed in a bay protected from wind and currents of Lago Calado, a várzea-lake with a continual connection to the main stream near the town of Manacapurú (Tab. 9). During the period from December to March it was so light that the values were equally true for the marginal and the central region. From April to June it was difficult to make a difference between the two regions because of water pools dispersed in them, so that samples were taken from the central region only from July onwards, when a largely closed plant-cover of almost 1 ha had developed. The varying density of the population can be seen from the great deviations in quantity of stem per m².

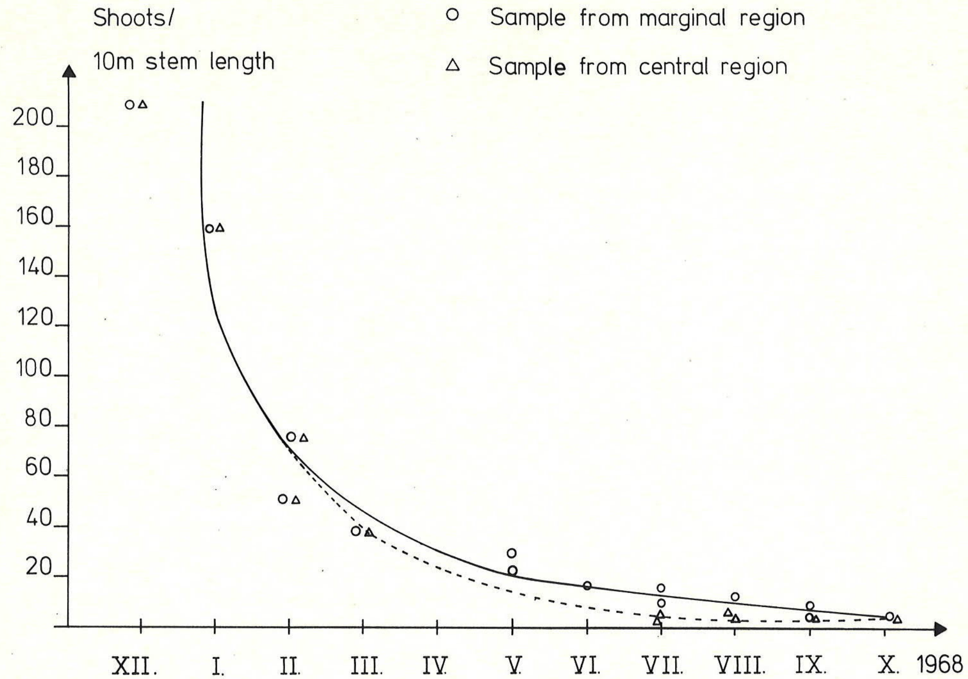

Fig.9: Number of shoots per stem length of Paspalum repens in Lago Calado

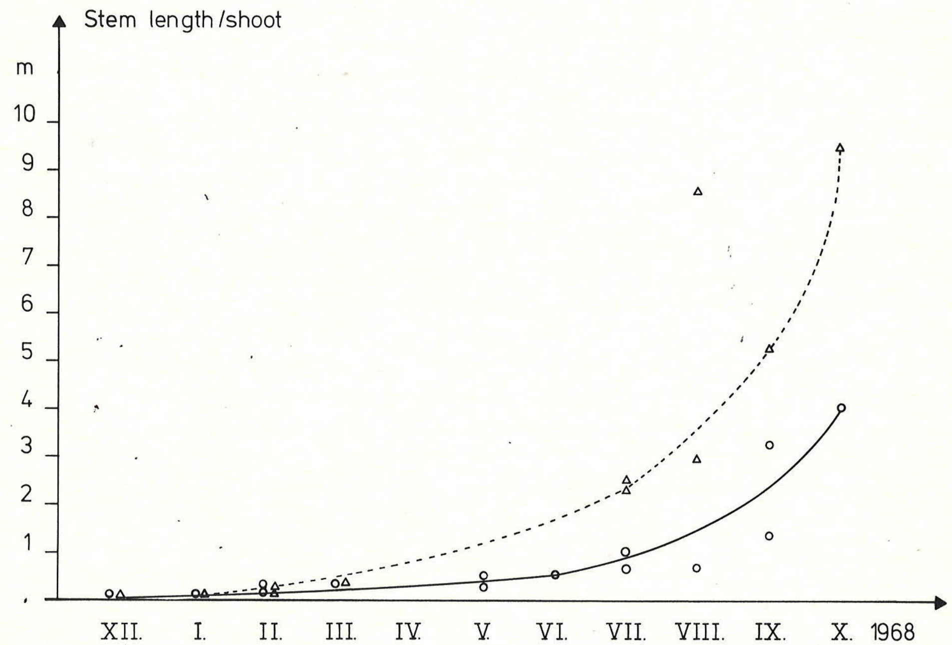

Fig.10: Stem length per shoot of Paspalum repens in Lago Calado

Figure 4 shows that the number of shoots in relation to the quantity of stems was highest in the months of December and January. At that time the plants, which had mainly developed from seeds, formed internodes of only 3—5 cm length. This made a quick ramification possible and furthered the vegetative growth. In February the growth of the whole population had changed. Internodes of 10 cm were formed. The number of shoots was reduced in relation to the present quantity of stems. This is especially obvious in the samples from the central region of the population. Here, we have a remarkably lower number of shoots per quantity of stems than in the marginal region, the age of this part being accordingly more advanced.

The change in the intensity of growth is expressed more clearly when the quantity of stems per shoot is drawn as a function of time (Fig. 10). Thereby it turns out that the quantity of stems per shoot shows an especially high increase in the central region from July/August onwards, whilst in the marginal region from September onwards the intensity of growth is simultaneously decreased. This depends on the flowering period which begins in the middle of June. In July already, parts of the panicles were ripe and dried up, and consequently the number of functionable shoots was noticeably reduced. In October the population had almost died, so that the quantity of stems per functionable shoot was extremely high, and partially the plants were already decaying.

Thus it is possible — as postulated at the beginning of the chapter — to see the development of the population from the relationship between shoots and quantity of stems per area. The higher the number of shoots per quantity of stems, the younger the population. The larger the quantity of stems in relation to the number of shoots, the slower it grows. This interpretation is confirmed by a comparison of the number of developed shoots per m² (Tab. 9). This number is reduced from 664 to 4. It must be pointed out here, that by this sort of direct comparison misinterpretations may easily result, as it does not take into account the total quantity of stems. A simple fictitious numerical example might make this clear:

	Total of stem length in m	shoots/m²	stem length in m/shoot	shoots/10 m stem length
Marginal sample 1 . . .	12,00	40	0,3	33,3
Marginal sample 2 . . .	3,00	10	0,3	33,3

Although sample 1 contains 40 shoots/m² and sample 2 only 10 shoots/m², the ratio of growth of the population is the same. The only difference is that in the first case the sample was taken from the denser part of the population.

Table 9: Relation of quantity of stem length to the number of shoots (Lago Calado)

Date	Sampling locality	stem length in m/m²	shoots/m² 1)	stem length in m/shoot	shoots/10 m stem length
5. 12. 67	MR2)	23,2	664	0,03	286,2
8. 1. 68	MR	6,8	108	0,06	158,6
15. 2. 68	MR	16,0	80	0,20	50,0
	MR	6,8	52	0,13	76,5
12. 3. 68	MR	14,8	56	0,26	37,8
11. 5. 68	MR	12,4	36	0,34	29,0
	MR	16,8	36	0,47	21,4
7. 6. 68	MR	9,6	16	0,60	16,7

Date	Sampling locality	stem length in m/m-	shoot/m² 1)	stem length in m/shoot	shoot0 mgn stoots/10 th
6. 7. 68	MR	30,0	28	1,07	9,3
	MR	12,4	20	0,62	16,1
	CR2)	83,4	36	2,32	4,3
	CR	30,4	12	2,53	3,9
10. 8. 68	MR	23,2	32	0,73	13,8
	CR	59,6	20	2,98	3,4
	CR	72,8	8	9,10	1,1
6. 9. 68	MR	39,6	12	3,30	3,0
	MR	11,4	8	1,43	7,1
	CR	84,8	16	5,30	2,1
4. 10. 68	MR	16,4	4	4,10	2,4
	CR	38,0	4	9,50	1,1

1) In this figure the thin hard sprouts, appearing newly around beginning of August, are not taken into account. They represent a special, well distinguishable form of development of the old and dense population, and cannot be compared with the original form of growth (compare p. 456ff.).

2) MR = Marginal region CR = Central region

Population B

The population developed in Lago Manacapurú, a várzea-lake with a continuous connection to the main river; there is always light current and every now and then there is a considerable influx of black-water.

From the stem-length/m² (Tab. 10) we can see that there was already in August a distinctly dense central region. The number of shoots in relation to the stem-length — as in population A — is reduced with advancing age (Fig. 11). This reduction, however, is not noticeable at the same high degree. Towards the end of the year there were more functionable shoots in the marginal as well as in the central region than in population A. Correspondingly it turns out that the relation between stem-length and number of shoots (Fig. 12), which represents the intensity of growth, is slightly reduced in September, this reduction is, however, by far less stronger than in population A. According to our expectations we find a smaller intensity of growth in the central region than on the margin, nevertheless at the same time it was considerably higher than in population A.

The results represent exactly the observed development of the population. Though the ratio of growth decreased from September onwards, the flowering period lasted until October, so that this population was still much fresher in October than population A, which had already completely ceased blooming.

Table 10: Relation of quantity of stem length to number of shoots (Lago Manacapurú)

Date	Sampling locality	stem length in m/m²	shoots/m² 1)	stem length in m/shoot	shoots/10 m stem length
8. 1. 68	MR2)	34,00	292	0,12	85,9
15. 2. 68	MR	12,00	108	0,11	90,0
	MR	14,00	84	0,17	60,0
12. 3. 68	MR	15,80	72	0,22	45,6
	MR	31,60	148	0,21	46,8
13. 4. 68	MR	24,40	108	0,23	44,3
	MR	21,60	108	0,20	50,0

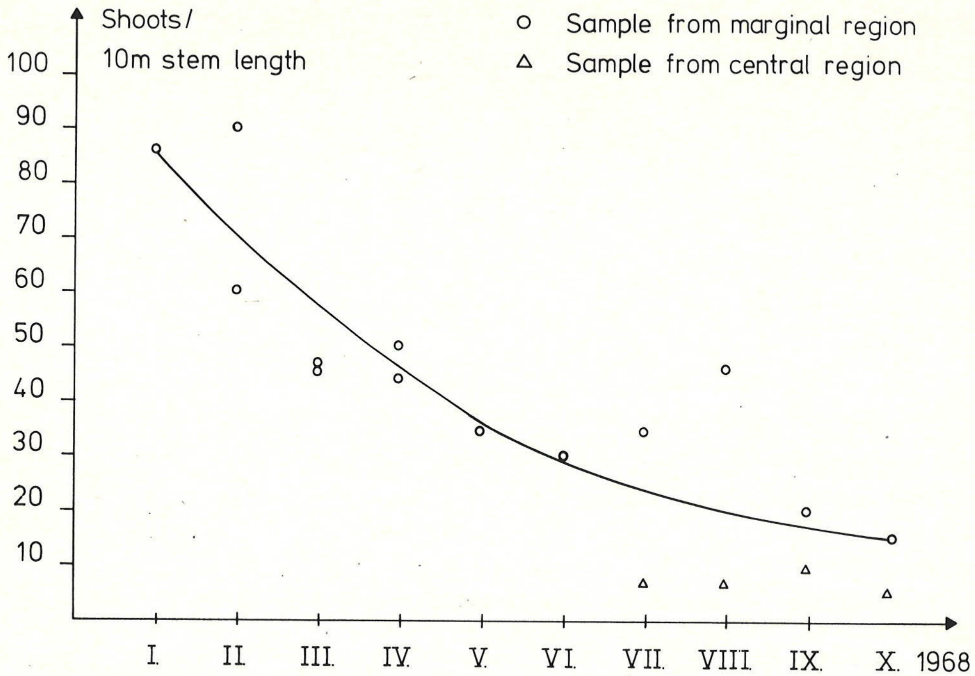

Fig.11: Number of shoots per 10m stem length of Paspalum repens in Lago Manacapurú

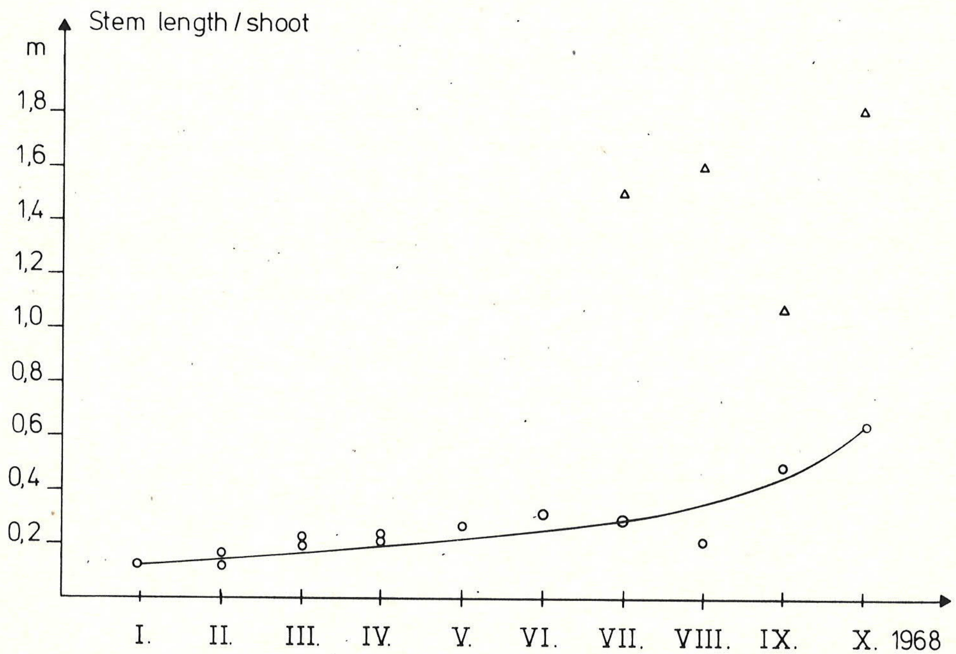

Fig.12: Stem length per shoot of Paspalum repens in Lago Manacapurú

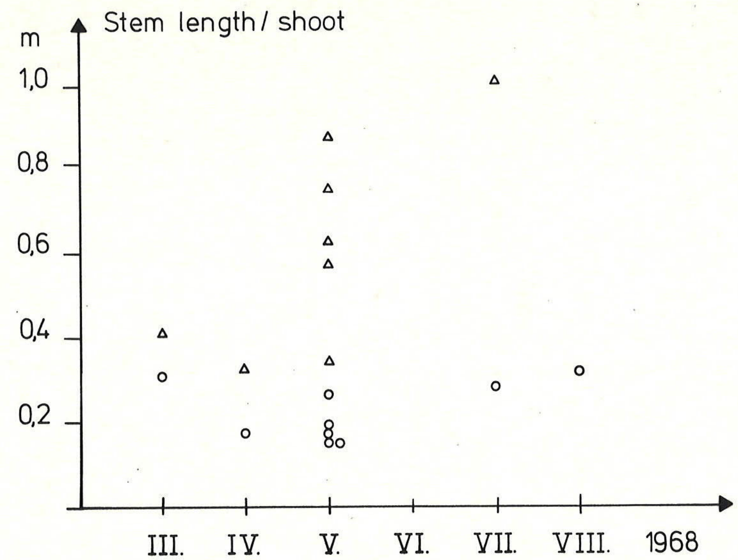

Fig.13: Stem length per shoot of Paspalum repens on Costa do Baixio

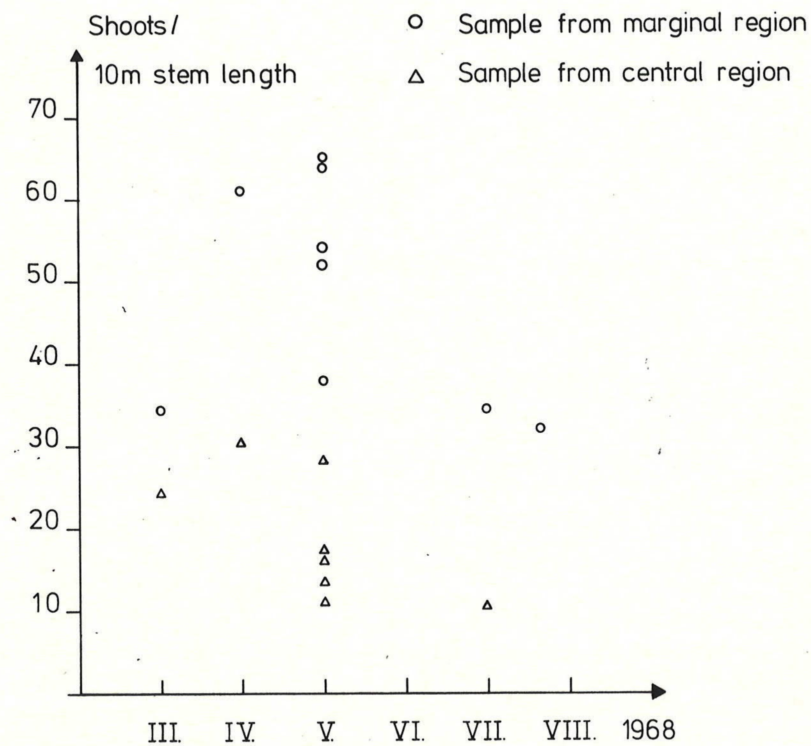

Fig.14: Number of shoots per 10m stem length of Paspalum repens on Costa do Baixio

Date	Sampling locality	stem length in m/m-	shoots/m² [1])	stem length in m/shoot	shem elm stem length
12. 5. 68	MR	19,60	72	0,27	36,7
7. 6. 68	MR	14,80	48	0,31	32,4
7. 7. 68	MR	19,60	68	0,29	34,6
	CR[2])	78,00	52	1,50	6,7
11. 8. 68	MR	18,80	88	0,21	46,8
	CR	70,00	44	1,59	6,3
7. 9. 68	MR	42,80	88	0,49	20,6
	CR	64,40	60	1,07	9,3
5. 10. 68	MR	20,40	32	0,64	15,7
	CR	28,80	16	1,80	5,6

[1]) In this figure the thin hard sprouts appearing newly from about October onwards are not taken into consideration. They represent a special, well distinguishable form of development of the old and dense population and cannot be compared with the original form of growth.

[2]) MR = Marginal region CR = Central region

In contrast of population A the development of population B was not yet finished. This prolongated period of development may depend on the chemistry of the water, and also on the good exchange of waters, caused by slight currents between the plants. Populations in other comparable várzea-lakes without currents had already finished their development in October like population A.

Population C

This population developed from March to August at the Costa do Baixio, a sedimentation zone of some square-kilometers on the Amazon. During the whole period of the development of the population there was a slight current up to 10 cm/sec. at the margin of the population. Besides during windy weather this area was exposed to considerable undulation.

According to stem-length shown in Table 11, a central region was formed. This, however, remained much lighter than that in the afore-treated populations. The relation between stem-length and shoots shows no remarkable alterations in the marginal region during the whole period (Fig. 13). The stem-length belonging to one shoot comes up to a maximum of 35 cm. Thus this region of the population was permanently in a young stage. In the central region the stem-length per shoot was a bit larger, being older, but the maximum length was only 1 m. Correspondingly, this is also valid for the intensity of growth, which is measured by the number of shoots per stem-length (Fig. 14). In the marginal region there are always more than 30 shoots per 10 m stem-length. This shows a high intensity of growth during the whole period. In the central region the July sample shows the lowest intensity of growth with regard to age.

The observed development of the population corresponds to the data shown in the figure. In their marginal region the plants had always leaves with blister-like swellings, which characterize a quickly growing young population. In the older interior region the bulbs were largely reduced. The thin hard sprouts and the decaying of the stems, such as found in the interior of the dense older populations, were not observed during the whole period, because the population was still too young and very thin. In August it was drifted away, except some single pieces of a few squaremeters, and in September even these had almost completely disappeared.

Table 11: Relation of quantity of stem length to number of shoots (Costa do Baixio)

Date	sampling locality	stem length in m/m²	shoots/m²	stem length in m/shoot	shoots/10 m stem length
2. 3. 68	MR[1])	30,60	92	0,33	30,1
	CR[1])	38,00	92	0,41	24,2
2. 4. 68	MR	34,00	208	0,16	61,2
	CR	44,00	132	0,33	30,0
3. 5. 68	MR	20,80	108	0,19	51,9
	MR	28,40	108	0,26	38,0
	MR	13,60	88	0,15	64,7
	MR	19,00	104	0,18	54,7
	MR	15,80	104	0,15	65,8
	CR	40,20	116	0,35	28,8
	CR	20,40	36	0,57	17,6
	CR	48,00	64	0,75	13,3
	CR	52,40	84	0,62	16,0
	CR	41,40	48	0,86	11,6
2. 7. 68	MR	32,20	112	0,29	34,8
	CR	56,00	56	1,00	10,0
1. 8. 68	MR	10,00	32	0,31	32,0

[1]) MR = Marginal region CR = Central region

Population D

This population grew up in the Paraná do Xiborena, an Amazon side branch near the mouth of Rio Negro, about 30 m wide. It was permanently exposed to currents. We did not make a difference between marginal and central region, for the population was at the most 5 m broad.

The relation between stem-length and number of shoots shows that (Tab. 12, Figure 10), the plants always remained in a young stage. Generally less than 30 cm stem-length were found per shoot.

Corresponding to this there are normally more than 40 shoots per 10 m stem-length (Fig. 15). That indicates a very high intensity of growth during the whole period.

The observed development confirms the trends given in the figure. During the whole period the plants had leaf-bases with blister-like swellings in their entire population and grew up quickly. A real central region could not be formed, for already after some weeks the main part of the plants were drifted away. This permanent alteration is also reflected in the figure.

The investigations of four *Paspalum repens*-populations made in different biotopes, show the possibility of presenting data on age and growth intensity by means of the relation between shoots and stem-length per unit area. This might be of importance in so far as a few samples allow us to state whether an important increase of organic matter can be expected or whether the production of the population examined has already stopped.

Table 12: Relation between quantity of stem-length and number of shoots (Paraná do Xiborena)

Date	sampling locality	stem length in m/m²	shoots/m²	stem length in m/shoot	shoots/10 m stem lengt
29. 12. 67	MR[1])	37,60	248	0,55	66
14. 1. 68	MR	46,60	376	0,12	81
22. 3. 68	MR	20,40	136	0,15	67
19. 4. 68	MR	15,00	136	0,11	91
23. 5. 68	MR	37,60	152	0,24	40
26. 6. 68	MR	21,60	56	0,38	26
24. 7. 68	MR	18,00	88	0,20	49
22. 8. 68	MR	47,20	284	0,16	60
19. 9. 68	MR	34,40	144	0,23	42

[1]) MR = Marginal region

Summary

Investigations on the "floating meadows" (Paspalo-Echinochloetum) of the várzea-region of central Amazonia in the surroundings of Manaus were made from May 1967 until October 1968. The ecology of the dominating species *Paspalum repens* Berg, *Paspalum fasciculatum* Willd., *Echinochloa polystachya* (H. B. K.) Hitchkock, *Leersia hexandra* Swart (Fam. Gramineae) and diverse subsidiary species (*Oryza perennis* Moench., *Hymenachne amplexicaulis* (Rudge) Nees, *Panicum chloroticum* Nees (Fam. Gramineae), *Scirpus cubensis* Poepp Kunth. (Fam. Cyperaceae) etc., was studied in details.

Regarding *Paspalum repens* Berg, various floating and one terrestrial forms of growth were observed. Further, quantitative investigations on primary production and the development of populations of this species were made. As shown by 4 *Paspalum repens*-populations which were growing under different environmental conditions, conclusions on age and rapidity of growth of the population could be drawn from the relation between quantity of stems and number of shoots.

The preliminary conditions for a "secondary colonization" of floating populations by non-floating plants and the repercussions of such sort of colonization on the primary populations are discussed.

The várzea-waters are subdivided into 3 biotopes with regard to the floating vegetation, and the factors reponsible for them are discussed:

1) Bank- and sedimentation-zones in the Solimões-Amazon.
   Dominating species: *Paspalum fasciculatum*, *Paspalum repens*, *Echinochloa polystachya*.

2) Várzea lakes with high fluctuations of water level.
   Dominating species: *Paspalum fasciculatum*, *Paspalum repens*, *Echinochloa polystachya*. Sometimes, however, as well all other mentioned species occur in masses. Biotope richest in species.

3) Várzea lakes with relatively little fluctuations of water level.
   Dominating species: *Leersia hexandra*, *Scirpus cubensis*, *Paspalum repens*.

Both the current-region of the Solimões-Amazon as a biotope of its own and the influence of black-water on the vegetation are discussed.

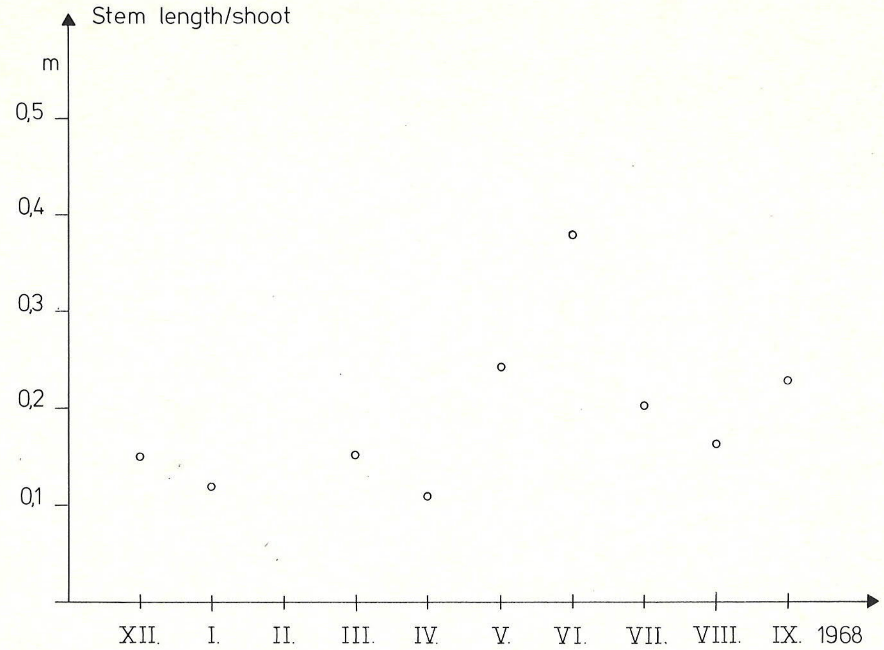

Fig. 15: Stem length per shoot of Paspalum repens in Paraná do Xiborena

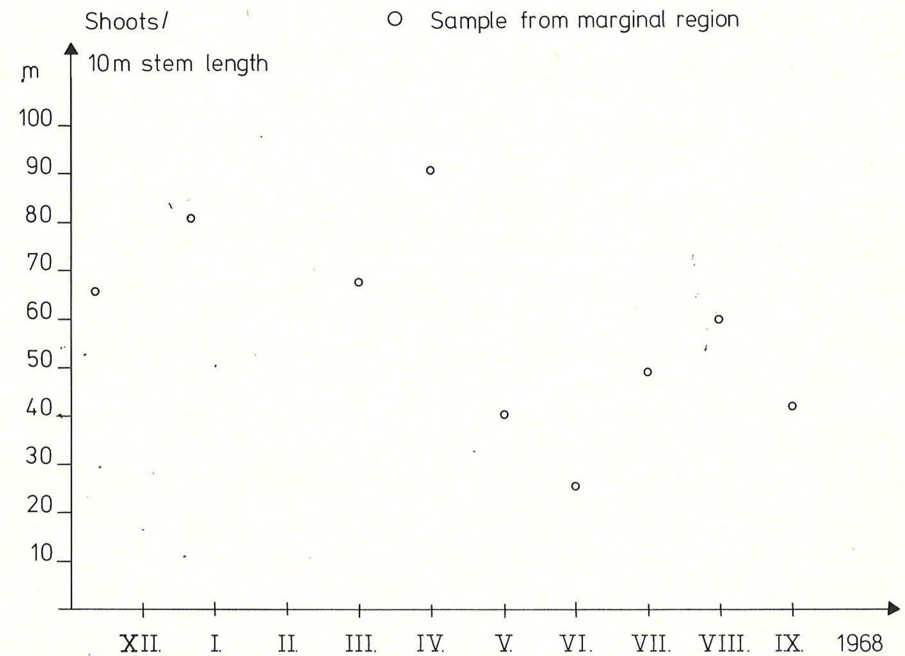

Fig. 16: Number of shoots per 10m stem length of Paspalum repens in Paraná do Xiborena

References

Agassiz, L. and E. C. Agassiz (1938): Viagem ao Brasil 1865—1866. — Brasiliana, São Paulo, Ser. 5, **95**: 654 pp.

Bard, J. (1965): Végétaux aquatiques tropicaux. — Revue Bois et Forêts des Tropiques **99**; janvier/février: 3—11.

Bennett, F. D. and H. Zwölfer (without year): Report on a survey of the insects and mites in northern South America undertaken in February—March, 1968. — Report. Commonwealth Institute of Biological Control, West Indian Station, Curepe, Trinidad: 29 pp.

Berg, A. (1961): Rôle écologique des eaux de la Cuvette congolaise sur la croissance de la jacinthe d'eau (*Eichhornia crassipes* (Mart.) Solms.) — A.R.S.O.M. Mémoires, Brüssel **12** (3): 1—120.

Black, G. A. (1950): Os capins aquáticos da Amazônia. — Bolm téc. Inst. agron. N., Belém-Pará **19**: 53—94.

Botsch, D. (1970): Auswirkungen und Ursachen epidemischer Wasserpflanzenausbreitungen. — Naturw. Rdsch., Stuttgart **23**: 323—324.

Chase, A. (1944): Grasses of Brazil and Venezuela. — Agriculture Am., Washington **4**:123—126.

Doell, J. C. (1877): Gramineae.-In: Flora Brasiliensis **2** (2). Ed. C. Fr. Ph. von Martius et al., Leipzig 1840-1906

Donselaar, J. van (1968): Water and marsh plants in the artifical Brocopondo Lake (Surinam, S. America) during the first three years of its existence. — Acta bot. neerl., Amsterdam **17** (3): 183—196.

Donselaar, J. van (1964): Botanical observations, 1964. — Biological Brocopondo Research Project, Surinam; Progress reports **1**: 16—18, 36—40, 56—38, 81—85.

Donselaar, J. van (1965): Botanical observations, 1965. — Biological Brocopondo Research Project, Surinam. Progress reports **2**: 99, 125—136.

Donselaar, J. van (1967): Botanical observations, 1966. — Biological Brocopondo Research Project, Surinam; Progress reports **3**: 181—195.

Donselaar, J. van (1969): Botanical observations, 1969. — Biological Brocopondo Research Project, Surinam; Progress report **4**, 247—248.

Ducke, A. and G. A. Black (1953): Phytogeographical notes on the Brazilian Amazon. — Anais Acad. bras. Cienc., Rio de Janeiro **25**: 1—46.

Geisler, R. (1969): Untersuchungen über den Sauerstoffgehalt, den biochemischen Sauerstoffbedarf und den Sauerstoffverbrauch von Fischen in einem tropischen Schwarzwasser (Rio Negro, Amazonien, Brasilien). — Arch. Hydrobiol., Stuttgart **66**: 307—325.

Gessner, F. (1955, 1959): Hydrobotanik. **1. 2.** Berlin, Deutscher Verl. der Wissenschaften: **517**, 701 pp.

Huber, J. (1909): Mattas e madeiras amazonicas. — Bolm Mus. para. "Emilio Goeldi", Belém, Pará **6**: 91—225.

Hueck, K. (1966): Die Wälder Südamerikas. Ökologie, Zusammensetzung und wirtschaftliche Bedeutung. — Stuttgart, Fischer: 422 pp.

Katzer, F. (1903): Grundzüge der Geologie des unteren Amazonasgebietes. — Leipzig, Weg: 296 pp.

Köppen, W. (1931): Grundriß der Klimakunde. — Berlin & Leipzig, de Gruyter: 388 pp.

Le Cointe, P. (1947): Arvores e plantas úteis. — Amazônia Brasileira 3. — Brasiliana, São Paulo, Ser. 5, **251**: 506 pp.

Lieth, H. (Edit.) (1962): Die Stoffproduktion der Pflanzendecke. — Stuttgart, Fischer: 156 pp.

Marlier, G. (1962): Étude sur les lacs de l'Amazonie centrale. — Cadern. da Amazônia, Manaus-Amazonas **5**: 51 pp.

Miranda, V. C. (1907/1908): Os campos de Marajó e a sua flora — considerados sob o ponto da vista pastoril. — Bolm Mus. para. "Emilio Goeldi", Belém, Pará **5**: 96—151.

Oliveira, A. I. and O. H. Leonardos (1943): Geologia do Brasil. — Ministerio de Agricultura, Rio de Janiero: 813 pp.

Reinke, R. (1962): Das Klima Amazoniens. — Mathem.-Naturw. Diss., Tübingen: 101 pp.

Schröder, R. (1955): Temperatur und Niederschlag in Brasilien. — Staden-Jahrbuch, Sao Paulo **3**: 7—18.

Sioli, H. (1950): Das Wasser im Amazonasgebiet. — Forschn. Fortschr., Berlin **26**: 274—280.

Sioli, H. (1956): Über Natur und Mensch im brasilianischen Amazonasgebiet. — Erdkunde, Bonn **10**: 89—109.

Sioli, H. (1967): Studies in Amazonian waters. — Atás do Simpôsio sôbre a Biota Amazônica, Rio de Janeiro **3**: 9—50.

Sioli, H. (1968): Principal biotopes of primary production in the waters of Amazonia. — Proc. Symp. Recent Adv. Trop. Ecol. Ed.: R. Misra and B. Gopal, Varanasi: 591—600.

Soares, L. de Castro (1956): Excursion guidebook. No 8. Amazônia. — Rio de Janeiro, International Geographical Union. Brazilian National Committee: 216 pp.

Spruce, R. (1908): Notes of a botanist on the Amazon and Andes. **1. 2.** Ed. by A. R. Wallace. London, Macmillan, 518, 542 pp.

Wallace, A. R. (1939): Viagens pelo Amazonas e Rio Negro. — Brasiliana, São Paulo, Ser. 5, **156**: 668 pp.